The relative importance of opposing drivers in determining population change in macaroni penguins *Eudyptes chrysolophus*

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Abstract

It is widely recognised that both nutrient-driven processes acting from the “bottom-up” and predator-driven processes acting from the “top-down” are important drivers of population change. However, studies that examine how these joint forces influence the population dynamics of oceanic species are lacking. In the Antarctic and Sub-Antarctic ecosystem, human-mediated changes have driven biological change at both ends of the food chain; rapid regional warming at the bottom and heavy exploitation of apex predator populations at the top. Consequently, many populations of marine predators have rapidly changed in size over the last 50-years. Unravelling the effects of bottom-up and top-down forcing on these open ocean ecosystems, has thus been highlighted as an immediate priority for polar scientists. The overall aims of this study were to use demographic, environmental and diet data to unravel the processes that contributed to a population of macaroni penguins at South Georgia declining rapidly between 1985 and 2012. I use mark–recapture modelling to examine the survival rates of macaroni penguins. Over 10 years, birds were marked with subcutaneous electronic transponder tags and re-encountered using an automated gateway system fitted at the entrance to the colony. These findings were combined with a 28-year time series of population counts and productivity measurements in an age-structured state-space population model to disentangle the processes underlying the observed population decline. Finally, I combined stable isotope analysis and tracking data to investigate the individual strategies macaroni penguins might employ to mitigate the effects of density-dependence during the breeding season. Macaroni penguins at South Georgia declined at 6% per year between 1985 and 2000, stabilising thereafter. This study indicates that the population declined in response to recruitment rates being lower than adult mortality. This trend was potentially accelerated by three large mortality events that were possibly associated with top-down predation pressure from giant petrels. Survival rates were low and variable during the fledging year, increasing to much higher levels from age 1 onwards. Year-to-year variability in demographic rates was induced by a combination of individual quality, top-down predation pressure and bottom-up environmental forces. The relative importance of these covariates on survival rates was age-specific, whereby predation pressure had a considerably greater effect during the fledgling year compared with birds older than 1-year. The population trajectory stabilised after 2000 in response to an increase in survival, as well as density-dependent feedbacks upon productivity. In order to minimise the effects of density-dependence during the breeding season and optimise daily energy expenditure, macaroni penguins appeared to make distinct dietary choices that remained highly consistent from year-to-year. Individually specialised foraging strategies

occurred in response to seasonal variations in foraging range, conspecific density and prey availability at the foraging sites. The future stability of this population will depend on the carrying capacity of the environment supporting productivity rates at their present level, and the population size and breeding success of giant petrels not increasing so that adult survival rates can remain stable. More broadly, this study highlights the importance of considering multiple causal effects across different life-stages when examining the demography of seabirds, and demonstrates the additional insights that can be gained by using models with increased precision.

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Horswill, C., J. Matthiopoulos, J. A. Green, M. P. Meredith, J. Forcada, H. Peat, M. Preston, P. N. Trathan and N. Ratcliffe. 2014. Survival in macaroni penguins and the relative importance of different drivers; individual traits, predation pressure and environmental variability. *Journal of Animal Ecology*, 83, 1057-1067. DOI: 10.1111/1365-2656.12229.

Ratcliffe, N., S. Crofts, R. Brown, A. Baylis, S. Adlard, C. Horswill, H. Venables, P. Taylor, P. N. Trathan and I. J. Staniland. 2014. Love thy neighbour or opposites attract? Patterns of spatial segregation and association among crested penguin populations during winter. *Journal of Biogeography*, 41, 1183-1192. DOI: 10.1111/jbi.12279.

Horswill, C., and P. N. Trathan. 2013. Macaroni penguin. *World Book Encyclopaedia*, US.

List of Conference Presentations

Horswill, C. *et al.* Dietary specialisation reflects changing constraints on foraging in the macaroni penguin. Oral presentation. Applications of Stable Isotope Techniques to Ecological Studies, Perth (2014).

Horswill, C. *et al.* The relative importance of different drivers influencing survival rates in macaroni penguins; individual traits, predation pressure and environmental variability. Poster presentation. International Statistical Ecology Conference, Montpellier (2014).

Horswill, C. *et al.* State-space modelling reveals the drivers of rapid population decline in macaroni penguins. Poster presentation. The Seabird Group, Oxford (2014).

Horswill, C. *et al.* Modelling survival variability in macaroni penguins. Oral presentation. Pacific Seabird Working Group, Alaska (2014).

Horswill, C. *et al.* Survival in macaroni penguins and the relative importance of different drivers. Oral presentation. International Penguin Conference, Bristol (2013).

Horswill, C. *et al.* Survival of macaroni penguins revealed using an automated gateway system. Poster presentation. BOU Avian Demography Conference, Leicester (2013).

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List of Accompanying Material

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Explanatory note on the text

Chapters three, five and six that are presented in the thesis were first prepared as manuscripts for submission to peer-reviewed journals. The publication status at the time of writing is indicated at the start of each chapter and those that are published presented in the Accompanying material. Only minor alterations have been made to the text of these chapters in order to improve the readability and overall coherence of the thesis. For this reason, there is a small amount of repetition in some of the methods and discussion sections of the thesis.

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I, Catharine Horswill, declare that, except where explicit reference is made to the contribution of others, that this dissertation is the result of my own work and has not been submitted for any other degree at the University of Glasgow or any other institution.

Signature _____

Printed name _____

List of Abbreviations

ANOVA - Analysis of variance

ANODEV – Analysis of deviance

AIC - Akaike Information Criterion

AIC_c - Second-order Akaike Information Criterion

CCAMLR - Convention on the Conservation of Antarctic Marine Living Resources

CMR – Capture-Mark Recapture

ENSO - El Niño Southern Oscillation

GLM – Generalised Linear Model

GPS – Global Positioning System

IPCC – Intergovernmental Panel on Climate Change

LRT - Likelihood ratio test

LSST – Local Sea Surface Temperature

MCMC – Monte Carlo Markov Chain

NOAA - National Oceanographic and Atmospheric Administration

PIT – Passive Integrated Transponder

PF – Polar Front

R – R: A language and environment for statistical computing

SACCF - Southern Antarctic Circumpolar Current Front

SAF - Sub-Antarctic Front

SAM – Southern Annular Mode

TAC – Total allowable catch

Chapter 1

Introduction

Population regulation

Although the abundance of most populations may fluctuate irregularly from year to year (May 1973; Royama 1977; Turchin 1995), the percentage change typically occurs within a narrow range compared to what reproductive and mortality rates would permit (Lack 1954). Stochastic variation around a dynamic mean implies that breeding numbers are regulated by factors that reduce the rate of population growth as numbers rise and increase the rate as numbers fall (Lack 1954). These stabilising density-dependent mechanisms prevent populations increasing without bounds, or declining to extinction. Potential regulatory processes will affect an increasing proportion of individuals as the population increases. In contrast, density-independent factors, such as extreme weather events, can affect a large proportion of the population regardless of its size, and result in large, unpredictable fluctuations that can destabilise a population (Newton 2013).

The predator-driven or "top-down" view of ecosystem control is widely accepted when considering terrestrial (Hairston *et al.* 1960, Fretwell 1977, Schmitz *et al.* 2000), fresh water (Carpenter *et al.* 1985, Northcote 1988) and intertidal ecosystems (Paine 1980). However, most ecosystem change in the open ocean, apart from those resulting from human exploitation, is thought to result from nutrient-driven or "bottom-up" control (Aebischer *et al.* 1990; Stenseth *et al.* 2002). Physical processes and nutrient fluxes dominate the structure and functioning of the open ocean (Behrenfeld *et al.* 2006). The prevailing view is therefore that top-down regulation in this system is unlikely (Pace *et al.* 1999). Despite this, the consequence of removing oceanic apex predators remains uncertain, and a number of studies have linked a change in the population size of pelagic predators to a marked change in community structure at lower trophic levels (Strong 1992;

Estes and Duggins 1995; Springer *et al.* 2003; Bascompte *et al.* 2005; Frank *et al.* 2005; Myers *et al.* 2007; Baum and Worm 2009; Springer and van Vliet 2014).

The influence of bottom-up regulation on the oceanic ecosystem is widely documented. Here, the principal mechanism is an effect of environmental variability on food availability. For seabirds, this relationship has been inferred for several species (Jenouvrier 2013). However, the methodological challenges of observing seabirds across large spatial scales and through unobservable life stages (e.g. for many seabird species colony attendance is limited between fledging and recruitment) has meant that early-life stages have been largely precluded from these studies (Baum and Worm 2009). Furthermore, this analysis is typically limited by the complexity of a system and the ability to collect data on relevant intrinsic and extrinsic processes. Therefore most biological change within the open ocean ecosystem has been examined within the context of a single variable that acts from either the top-down or the bottom-up. Few studies have considered these effects in unison (but see Laws 1977; Estes and Duggins 1995; Frank *et al.* 2005; Myers *et al.* 2007; Springer and van Vliet 2014), and even fewer have assessed their relative importance over different life-history stages (see Schwarz *et al.* 2013).

The polar ecosystem

In theory, the demographic parameters of polar organisms will have been selected to cope with the strong climate variability that is characteristic of this ecosystem (Clarke *et al.* 1996; Forcada *et al.* 2008). However, certain processes may potentially be more sensitive than others. For example, in long lived species, adult survival is predicted to be less variable in response to environmental change compared to juvenile survival and breeding success; i.e. adult survival is more environmentally canalized (Gaillard and Yoccoz 2003). Widespread population declines of upper-level predators across this region have highlighted the necessity to disentangle the influence of bottom-up and top-down forcing on different demographic processes (Smetacek and Nicol 2005).

The early view was that pelagic food chains in the Polar Regions were short, involving comparatively few species, i.e. they were characterised by a large prey resource supporting an assemblage of apex predators (Laws 1977). However, research conducted over the past few decades has shown this concept to be overly simplistic. For example, the phylogenetic diversity of plankton in these regions are equivalent to temperate climate zones (López-García *et al.* 2001), implying that the structure and functioning of open ocean ecosystems

are broadly similar across all latitudes (Smetacek and Nicol 2005). Furthermore, an increasing number of studies have demonstrated that the demography of particular "apex" predators is driven by factors operating at trophic levels that are both above and below (Boveng *et al.* 1998; Reid *et al.* 2013; Schwarz *et al.* 2013). By considering these predators as occupants of intermediate trophic levels, we establish a more robust framework in which to evaluate the opposing drivers of their population dynamics.

The polar ecosystem has received increasing attention due to human-mediated changes driving biological change at both ends of the food chain (see Chapter 2 for review). Rapid regional warming has been associated with changes across multiple trophic levels of the ecosystem (Clarke *et al.* 2007; Ducklow *et al.* 2007), whilst heavy exploitation of apex predator populations has removed a major component of upper trophic-level biomass (Kock 1992; Agnew 2004). Understanding how populations of oceanic predators are responding to these changes, and quantifying the relative importance of bottom-up and top-down forcing to population change is thus considered an urgent task (Smetacek and Nicol 2005).

Macaroni penguins

The macaroni penguin (*Eudyptes chrysolophus*) is the most abundant penguin species in the world, and one of the most important avian marine consumers in the Sub-Antarctic region. They are reported to consume more prey than any other seabird species in this ecosystem (de Brooke 2004); at South Georgia (in the South Atlantic Ocean) this equates to ~8 million tonnes of krill annually (Boyd 2002). At South Georgia, populations experienced rapid population growth during the mid-1900s (Croxall and Prince 1979), but between the late 1970s and early 2000s the net population declined by *c.* 70% (Trathan *et al.* 2012). During the same time period, numbers at Marion Island (in the southwest Indian Ocean) declined by a similar amount (*c.* 70% at 3 colonies, Crawford *et al.* 2006). In contrast, numbers breeding at the Kerguelen Islands (in the central south Indian Ocean) increased during the 1970s and 1980s (Weimerskirch *et al.*, 1989); more recent trends for this population have not been published. Previous studies on macaroni penguins have linked environmental covariates with their short-term population trajectory. Here the proposed mechanism is an effect on reproductive performance (Reid and Croxall 2001; Forcada and Trathan 2009). The links between individual covariates (such as environmental variability), demographic rates, and the overall population trajectory remain poorly understood.

This thesis utilises data collected from the colony at Fairy Point, Bird Island, South Georgia (54° 00' S, 38° 03'W) between 1985 and 2012 (*c.* 1417 pairs in 1985; *c.* 493 pairs in 2012). Colonies at Bird Island were monitored infrequently between 1958 and 1985, but Fairy Point became part of a dedicated long term monitoring program in 1985, collecting annual population counts and productivity measurements. A capture-mark-recapture (CMR) project was initiated in 1986 using flipper bands and ran for 3 years. This program stopped following anecdotal evidence of links between banding and reduced survival rates. This relationship was later supported by studies on other penguin species (e.g. Froget *et al.* 1998). A CMR program was reinstated in 2003 based on passive integrated transponder (PIT) tags (Texas Instruments, USA; www.ti.com/lit/ds/symlink/ri-trp-ir2b.pdf) (Chapter 3). The colony of macaroni penguins at Fairy Point has been included in a number of independent studies, such that many aspects of their breeding biology and behavioural ecology are well understood. These include telemetry (e.g., Croxall *et al.* 1993; 1999; Trathan *et al.* 2006; Barlow *et al.* 2002; Barlow and Croxall 2002a; Green *et al.* 2006; 2009; Hart *et al.* 2010; Waluda *et al.* 2010) and stable isotope studies (Bearhop *et al.* 2006). The nearby colony of macaroni penguins at Gold Crest Point, Bird Island, South Georgia, has also been included in a long-term study of diet through identification of stomach contents collected during the crèche phase of the breeding season (Waluda *et al.* 2012). As individuals from Gold Crest and Fairy Point are known to forage within similar areas during the brood-guard stage of the breeding season (Trathan *et al.* 2006), these data can be used to examine the inter-annual dietary variation of both populations.

Antarctic krill

In a general breeding season, the diet of macaroni penguins at South Georgia is dominated by Antarctic krill (Waluda *et al.* 2012). At South Georgia the krill stock is not thought to be self-sustaining but is dependent on immigration from spawning grounds further south. Individual krill are then resident at South Georgia for several years, forming an important food source for the many predators that breed in this area (Agnew 2004). Large-scale fluctuations in the biomass of krill at South Georgia can occur between years (Priddle *et al.* 1988). Linkages between krill density and yearly sea ice extent have been identified (Atkinson *et al.* 2004) and are thought to result from the greater winter feeding habitat offered by extensive sea ice, and the effect of sea-ice melt on the subsequent spring bloom. The relationship, however, is not simple and there are both annual and regional exceptions (Loeb *et al.* 1997; Constable *et al.* 2003; Hewitt *et al.* 2003). The overall trend of krill density for this region is also difficult to verify. Net-based surveys have indicated a

potential 80% decline in krill density in the southwest Atlantic between 1976 and 2004 (Atkinson *et al.* 2004); while acoustic surveys from the same region show similar episodic declines in abundance but no overall trend through the time series (1981-2002, Hewitt *et al.* 2003). Further investigation is needed to standardise methodology and compare long-term krill density observations in the Southern Ocean (Fielding et al. 2014). Antarctic krill have also been part of a dedicated fishery since 1962 (Kock 1992; see Chapter 2; Table 1).

Thesis aims

This study aims to use demographic, diet and environmental data to separate the demographic processes that contributed to the number of macaroni penguins at South Georgia rapidly declining between 1985 and 2012, and examine how these processes are influenced by opposing drivers. To identify potential bottom-up drivers, recent environmental and human-mediated changes at South Georgia are reviewed in Chapter 2. Then in Chapter 3 and Chapter 4 I use mark–recapture modelling to examine the survival rates of macaroni penguins. These birds were marked with subcutaneous electronic transponder tags and re-encountered using an automated gateway system fitted at the entrance to the colony. Specifically the aims of these chapters were:

1. To determine the principal drivers of year-to-year variation in the survival rates of macaroni penguins and how this changes with age;

2. To describe quantitatively the relative importance of the different drivers that influence the survival rates of macaroni penguins.

In Chapter 5 I use a state-space demographic model to separate the processes underlying the observed decline in this population of macaroni penguins. This framework permits missing data to be imputed as a function of the covariates and demographic processes (Buckland *et al.,* 2004). The aims of this chapter were as follows:

3. To model historic survival rates of macaroni penguins as a function of influential drivers in an integrated population model;

4. To determine the principal drivers of year-to-year variation in the productivity rates of macaroni penguins;

5. To describe quantitatively the relative importance of different covariates influencing the population trajectory of macaroni penguins between 1985 and 2012.

Chapter 6 examines how macaroni penguins might mitigate the impacts of intra-specific competition that were highlighted in Chapter 5. To do this I use stable isotope and tracking data. The aims of this chapter were:

6. To investigate individual variation in the diet of breeding macaroni penguins and examine how this varies as a function of sex, breeding parameters and foraging constraints;

7. To determine whether individuals specialise in their dietary choices across years.

Finally, in Chapter 7 I present a synthesis and discussion of my results in the context of environmental and human-mediated changes in this ecosystem.

Chapter 2

Environmental and human-mediated change in the South Georgia ecosystem

This chapter reviews environmental and human-mediated changes that have occurred in the South Georgia marine ecosystem in order to identify candidate bottom-up drivers that may have influenced the demographic parameters of macaroni penguins (*Eudyptes chrysolophus*) at Bird Island. The focus is on exploitation activities that have been linked to population changes in species that compete for the same prey resource, and environmental effects that are linked to local productivity. For environmental changes, the time period considered was determined by the advent of satellite remote sensing (1980s to present), and for exploitation activities the time period considered was determined by reported information on total catches (1790 to present).

Environmental change

Ocean-scale forces

El Niño/Southern Oscillation (ENSO) is a major mode of coupled atmosphere-ocean variability that operates on inter-annual timescales. Whilst ENSO is triggered in the equatorial/tropical Pacific it has teleconnections to the Southern Ocean and Antarctica via both atmospheric and oceanic processes (Turner 2004). Since the late 1970s, the canonical eastern Pacific El Niño has become less frequent and El Niño Modoki has become more common (Ashok *et al.* 2007; Yeh *et al.* 2009). As these events differ in both the location of maximum sea surface temperature (SST) anomalies and tropical–midlatitude teleconnections (Ashok *et al.* 2007), linkages to the Southern Ocean and Antarctica via atmospheric and oceanic processes are also likely to differ (Lachlan-Cope and Connolley

2006). During an El Niño Modoki event, a positive value of ENSO is immediately associated with cooler SSTs at South Georgia; followed by warm SST anomalies after 1.5-2 years (Meredith *et al.* 2008). An increase in SST influences oceanic advection and upwelling resulting in lower levels of local chlorophyll *a* and primary productivity (Behrenfeld *et al.* 2006). Between 1983 and 2008, ENSO had a marked preponderance of El Niño events compared with La Niña events. This was predominantly driven by large El Niños in 1983, 1987, 1992 and 1998 (Meredith *et al.* 2008).

The Southern Annular Mode (SAM) is the dominant mode of extra-tropical variability in the Southern Hemisphere. It is characterised by shifts in atmospheric mass between a node centred over Antarctica and a ring encompassing the lower latitudes. SAM fluctuates on timescales of weeks to decades, including inter-annual periods, and is associated with variations in the circumpolar winds over the Southern Ocean (Sengupta and England 2006). A positive phase of the SAM is associated almost immediately with warm SST anomalies at South Georgia (at time lags of ~1 month) (Meredith *et al.* 2008). SAM has also showed a higher index-state (i.e. stronger circumpolar winds) during recent decades (Thompson *et al.* 2000). This has been attributed at least partially to human-mediated changes, such as greenhouse gas emissions and ozone depletion (Marshall *et al.* 2004; Thompson and Solomon 2002).

Temperature

The Antarctic Peninsula has shown some of the clearest signals of regional warming in the world. In the last 40 years the mean annual air temperature has increased 2.8^{o}C causing declines in sea ice extent (Vaughan *et al.* 2003; Stammerjohn *et al.* 2008). However, the SST at South Georgia showed a small negative trend during the 1980s and 1990s, equivalent to a cooling of 0.14^{o}C (Meredith *et al.* 2008). Although the change in atmospheric temperatures correlates with the trend observed in SAM, the change in SST is in the opposite direction. Therefore it is more likely that ENSO and other climate-scale processes have dominated the SST change near South Georgia during this period (Meredith *et al.* 2008).

Commercial exploitation of marine fauna

Over the past 200 years, a major component of upper trophic-level biomass has been removed from the South Georgia ecosystem (see Figure 1 for timeline). A brief description of each activity and target species are given below and are summarised in Table 1.

Sealing (1780s -1965)

Commercial sealing operations began at South Georgia in the 1790 targeting Antarctic fur seals (*Arctocephalus gazella*) for their skins and southern elephant seals (*Mirounga leonina*) for their blubber. By the 1820s, exploitation of fur seals at South Georgia was deemed uneconomical (Agnew 2004). It was estimated that 1.2 million fur seal skins were taken during this time (McCann and Doidge 1987). Sealing efforts were then refocused to the South Shetland Islands (McCann and Doidge 1987). Sporadic exploitation of the populations at South Georgia occurred as populations recovered and strict licensing was instigated in 1905 (Agnew 2004). After 1905, harvesting of fur seals was prohibited, and exploitation of elephant seals was managed using quotas and spatial closures (Agnew 2004). Although this management was effective and sustainable, the industry closed in 1965 (Agnew 2004). Rapid population growth of fur seals occurred between the late 1950s and the 1980s (Boyd 1993); populations increased by 16.8% annually to reach levels potentially in excess of pre-exploitation numbers (Bonner 1985; McCann and Doidge 1987). Elephant seals are thought to have returned to pre-exploitation numbers by the early 1900s, and populations do not appear to have changed since the termination of commercial exploitation in 1965 (Boyd *et al.* 1996).

During the sealing era king penguins (*Aptenodytes patagonicus*) were also exploited for oil. Evidence for smaller species being exploited, such as macaroni penguins, is less clear, but depredation by the sealers for food is likely (Croxall 1992). In the Chatham Islands, New Zealand, local extinction of penguin populations occurred in parallel to the sealing efforts, and is likely to have been driven by depredation of birds and eggs (Falla 1962).

Whaling (1904 – 1986)

The whaling industry progressed following the decline of sealing in the early 1900s, and whaling stations at South Georgia were a major focus of the Southern Ocean industry throughout the early 1900s (Gambell 1987). However, following the introduction of large factory ships that could process whales away from land stations, uncontrolled expansion of the industry occurred (Agnew 2004). Whilst regulatory bodies set restrictions, the industry harvested significantly above sustainable limits from the 1960s onwards, and overexploitation lead to widespread population declines (Agnew 2004). Following a memorandum, many whaling countries ceased efforts in 1986 (Agnew 2004). Population recovery for some species has been slow, such as blue whales (*Balaenoptera musculus*),

but other species are thought to have shown evidence of strong recovery (humpback whales *Megaptera novaeangliae*; Clapham *et al.* 1999).

Commercial fisheries (1960s to present)

Following the decline of the sealing and whaling industry, commercial fishing started around South Georgia in the 1960s (Agnew 2004). The USSR fleet was active in these waters from 1962, but throughout the 1960s the statistics only cover catches of marbled rockcod (*Notothenia rossii*). It is quite likely that these were under-reported and that other species were also targeted (Agnew 2004). During the 1970s and early 1980s fisheries at South Georgia operated without catch limits and were "boom and bust", exploiting new species as others became uneconomical (Agnew 2004). Against a background that overfishing might have serious consequences for the Antarctic, The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) was negotiated during 1979-80 and came into force in 1982 (Edwards and Heap 1981). Each fishery that removed over 10,000 tonnes from Area 48.3 (South Georgia) between 1970 and 2002 is reviewed below (total catches are summarised in Figure 2). There is also a focus on the position of the target species in the food web; whether the target species eat krill and are a prey species of other marine predators in this ecosystem. To assess their importance as a prey species, I examined diet data for two of the most abundant marine predators; macaroni penguins and Antarctic fur seals. I used two studies that assessed the breeding season diet from 1989 to 2010 for macaroni penguins (Waluda *et al.* 2012) and from 1991 to 2004 for Antarctic fur seals (Reid *et al.* 2006). The absence of formerly harvested fish species from their diets may therefore indicate limited population recovery of fish stocks, rather than predators preferring alternative prey.

The marbled rockcod was the first target species of the South Georgia fishery. First catches were recorded in 1969 (Agnew 2004), and stocks were heavily depleted by the early 1970s (Kock *et al.* 2004). Stocks were depleted to about one tenth of the pre-exploitation level by the time the fishery closed in 1985 (Burchett and Ricketts 1984), and population recovery is thought to be limited (Kock *et al.* 2004). At South Georgia, the diet of marbled rockcod varies considerably during its life-cycle, but the main food of adults is krill (Tarverdiyeva 1972; Burchett 1983). During the adult stage, individuals are found offshore, aggregating in submarine canyons around South Georgia (Agnew 2004). Juveniles are seasonally important to blue-eyed shags (*Phalacrocorax atriceps bransfieldensis*) (Casaux and Barrera-Oro 1993), and are also found in the diet of Antarctic fur seals (Reid and Arnould

1996) and elephant seals (Daneri and Carlini 2001). There is no evidence of marbled rockcod in the diet of macaroni penguins during the breeding season (Waluda *et al.* 2012).

The mackerel icefish (*Champsocephalus gunnari*) was one of the most important species caught at South Georgia between 1976 and 1990 (Agnew 2004). Stock size in the early 1990s was low compared with the 1970s-1980s, but following the cessation of the fishery the stock has continued to fluctuate substantially with episodic dramatic declines in abundance (Everson *et al.* 2001). The fishery reopened in 1996 with regulations on catch limits (CCAMLR 2013). Mackerel icefish are distributed throughout the shelf area of South Georgia (Frolkina 2002) and the adults feed primarily on krill, changing to the amphipod *Themisto gaudichaudii* during years when krill availability is reduced (Kock *et al.* 1994). This species is seasonally important to Antarctic fur seals (Reid *et al.* 2006) and macaroni penguins (Waluda *et al.* 2012), especially during years when the abundance of krill is reduced.

The fishery for South Georgia icefish (*Pseudochaenichthys georgianus*) had low initial catches, but increased in 1977 after the mackerel icefish fishery became less economical (Agnew 2004). The fishery closed in 1990 (Clarke *et al.* 2008), although the species still appears as bycatch in the commercial mackerel icefish and krill fisheries (Ross *et al.* 2006). A bycatch limit was implemented in 1993 (CCAMLR 1989-2013). Heavy exploitation in the late 1970s is thought to have decreased the stock to about 24-40% of its level in 1976 (Kock 1992), and the population is thought to have remained lower than pre-exploitation levels (Clarke *et al.* 2008). South Georgia icefish are distributed throughout the South Georgia shelf and the summer diet of adults is dominated by Antarctic krill (Clarke *et al.* 2008). South Georgia icefish are seasonally important to macaroni penguins and fur seals (Reid *et al.* 2006; Waluda *et al.* 2012).

The grey rockcod (*Lepidonotothen squamifrons*) was targeted with low commercial importance from the 1960s, and the fishery was closed in 1989. The current stock status is unknown (Kock 1992). Grey rockcod are widely distributed across the South Georgia shelf region. During the summer and in shallower water salps dominate the diet, but in the winter and at depths >350 m amphipods and krill are dominant (Gregory *et al.* 2014). Grey rockcod have not been detected in the diet of fur seals or macaroni penguins during the breeding season (Reid *et al.* 2006; Waluda *et al.* 2012).

Catches of humped rockcod (*Gobionotothen gibberifrons*) followed a similar course to the South Georgia icefish with low initial catches followed by an increase in 1977 (Kock 1992). Stocks declined significantly during the late 1970s and the fishery was closed in 1989 (Kock 1992). Rates of population recovery are unknown. Humped rockcod are distributed throughout the continental shelf of South Georgia and krill are a dominant part of the adult diet (Targett 1981). They have not been identified in the macaroni penguin diet, but are noted in the diet of fur seals during the breeding season (North 1996).

The Patagonian rockcod or yellow-fin notothen (*Patagonotothen guntheri*) was fished commercially at South Georgia between 1979 and 1990 (Collins *et al.* 2008). The stock fluctuated substantially during this time, but exact population trends are unknown (Kock 1992). This species is abundant at Shag Rocks (north-western tip of South Georgia), but is predominantly absent from the rest of the South Georgia shelf (Collins *et al.* 2007). The diet of juvenile fish is dominated by copepods, whilst adult fish principally consume the amphipod (*Themisto gaudichaudii*) and krill (Collins *et al.* 2008). They are the main prey of Patagonian toothfish and are also seasonally important to white-chinned petrels (Berrow and Croxall 1999), black-browed and grey-headed albatross (Reid *et al.* 1996). However, they do not appear in the diets of macaroni penguins or Antarctic fur seals at South Georgia (Reid *et al.* 2006; Waluda *et al.* 2012).

The Patagonian toothfish (*Dissostichus eleginoides*) is currently one of the most important species of the South Georgia fishery and has been targeted since 1989. The stock declined to around one tenth between 1989 and 2005, although the majority of this decline took place between 1989 and 1995 (CCAMLR 2012). The fishery has also been linked to large-scale by-catch of Procellariiformes (albatrosses and diving petrels) that exploit the discards of this fishery (Kock 1992). Adult Patagonian toothfish are mainly distributed on the continental slope (500m depth) and their main prey is Patagonian rockcod. In contrast, larvae and juveniles are found in coastal waters during summer and their main prey is krill (García de la Rosa *et al.* 1997). Patagonian toothfish have not been detected in the diet of fur seals or macaroni penguins at South Georgia (Reid *et al.* 2006; Waluda *et al.* 2012).

Lantern fish or myctophids were first targeted in the 1980s and were part of an unrestricted fishery until 1992 (CCAMLR 1989-2013). The fishery peaked in the late 1980s and early 1990s (Agnew 2004), and was closed in 2003 (CCAMLR 2013). In 1993, catches around South Georgia mainly included *Krefftichthys anderssoni* and *Electrona carlsbergi*,

however the wider Myctophidae group are also an abundant by-catch species of the commercial krill fishery operating in the area north and northwest of South Georgia (Iwami *et al.* 2011). The current stock status is unknown, however stocks are thought to have declined between the late 1970s and early 1990s (Kock 1992). Krill are only consumed by the larger myctophid species, which represented a numerically minor part of the myctophid community (Shreeve *et al.* 2009). Myctophids are thus thought to provide a krill-independent link between secondary production and higher trophic levels (Shreeve *et al.* 2009). In the Southern Ocean, myctophids are the primary prey of king penguins (Olsson and North 1997), elephant seals (Cherel *et al.* 1993; 2008) and the squid *Martialia hyadesi* (Rodhouse *et al.* 1992). They are also seasonally important to fur seals and macaroni penguins (Reid *et al.* 2006; Waluda *et al.* 2012).

Antarctic krill were first targeted in the 1962 and small catches were continued throughout the 1960s. A permanent fishery at South Georgia started in 1972 and full-scale commercial operations commenced in the mid-1970s (McElroy 1984). Catch limits were unrestricted until 1992 (CCAMLR 1989-2013). South Georgia is one of the most important fishing grounds (Kock 1992) despite operating only during winter (Everson and Goss 1991); the fishery moves south with the retreating ice during the summer. Harvesting peaked in 1982, underwent a major decline between 1983 and 1985, before rising and remaining relatively constant from 1986 onwards (Kock 1992). Krill form a major component of the year-round diet for many Antarctic predators, including, fish, seals, fur seals, whales, penguins, albatross and giant petrels (Tarverdiyeva 1972; Targett 1981; Burchett 1983; Kock *et al.* 1994; Reid and Arnould 1996; García de la Rosa *et al.* 1997; González-Solís *et al.* 2000; Collins *et al.* 2008; Shreeve *et al.* 2009; Waluda *et al.* 2012; Gregory *et al.* 2014).

Summary

Although harvesting of macaroni penguins during the sealing era was unreported, it seems likely that colonies close to sealing beaches would have been negatively affected by depredation. Increased levels of krill biomass associated with the large-scale removal of whales and fish are then likely to have positively influenced their population size during the mid-1900s. This thesis aims to assess the mechanisms that have contributed to the population trajectory between 1985 and 2012. This period of population decline coincides with changes in the preponderance of El Niño events, increases in the SAM, as well as localised decreases in SST. It also coincides with the population recovery of Antarctic fur seals and whales, as well as intensive fishing activities during the early part of the study,

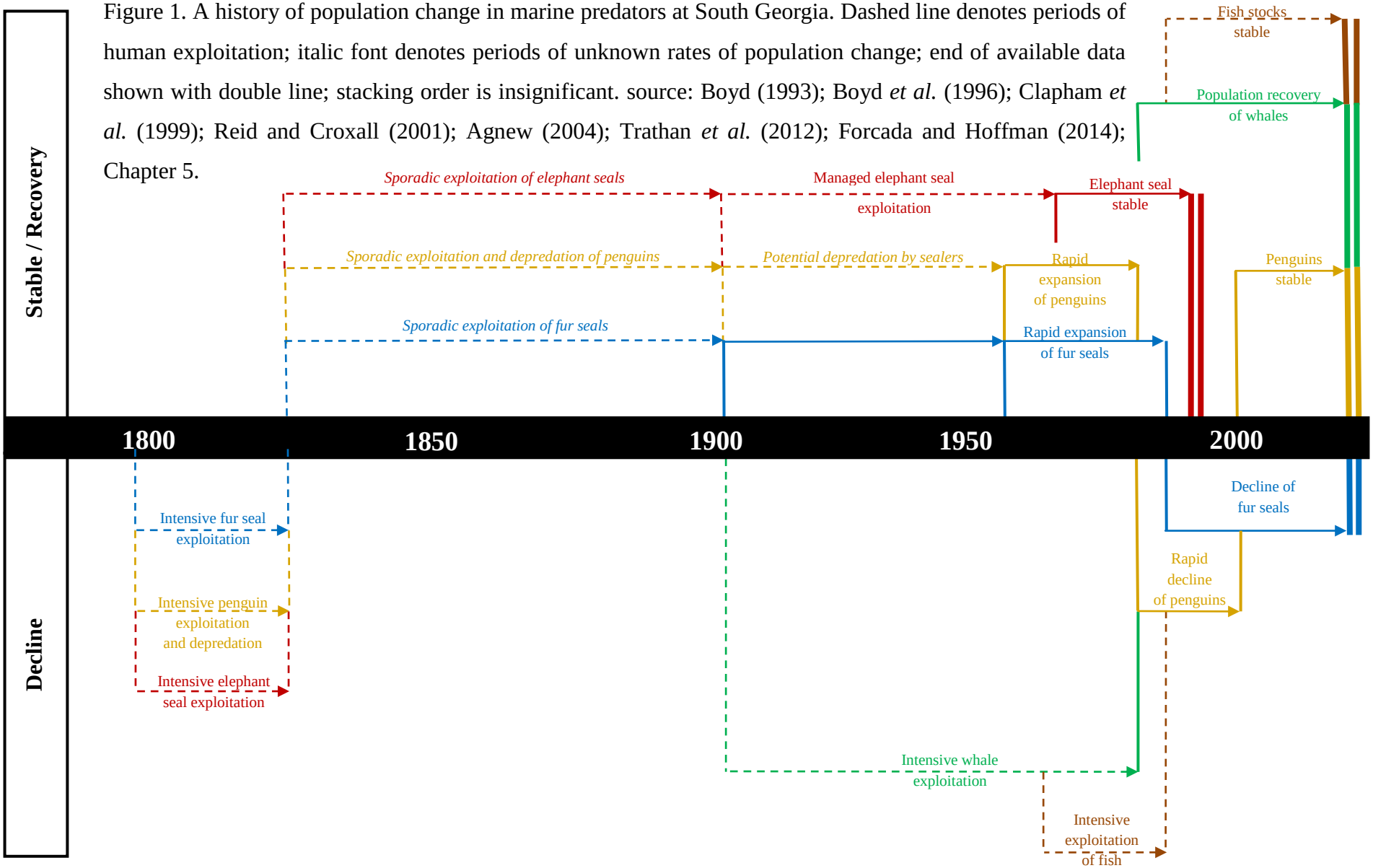
especially of key prey species (mackerel icefish, South Georgia icefish, myctophids and Antarctic krill). This was reduced to myctophids and Antarctic krill only from the early 1990s onwards. For the scope of this thesis, I will explore the influence of bottom-up regulation using ENSO, SAM and SST, as well as competition with fur seals and conspecifics. Due to lack of available data, potential links with recovering whale and elephant seal populations are not assessed. Furthermore, given the low year to parameter ratio, it was not possible to evaluate competition with individual fisheries. However, potential links with these variables are qualitatively evaluated in Chapter 7 within the context of the overall results.

Table 1. The history of human exploitation activities at South Georgia and a consideration of the target species position in the food web in relation to the prey species krill and predators macaroni penguins (MP) and Antarctic fur seals (FS) (Kock 1992; Reid *et al.* 2006; Waluda *et al.* 2012; CCAMLR 1989-2013).

Fishery	Catches first recorded	Closure	TAC	Fishery reopened	Seasonal closure	Impact to stock	Stock recovered	Krill in diet (≥1 life stage)	Diet of MP	Diet of FS
Antarctic fur seal	1790	1820s	-	-	-	H	Y	Y	N	-
Elephant seal	1790	1965	1905	-	-	H in 1800s; S in 1900s	Y	Y	N	N
Whales	1904	1986	1905	-	-	H	ss	Y	N	N
Marbled rockcod	1969	1985	1988	-	-	H	N	Y	N	N
Mackerel icefish	1976	1990	1988	1996	1996	H	U	Y	Y	Y
South Georgia icefish	1977	1991	1988	-	-	H	N	Y	Y	Y
Grey rockcod	1960s	1989	1988	1991	-	U	U	Y	N	N
Humped rockcod	1976	1989	1988	-	-	H	N	Y	N	Y
Patagonian rockcod	1979	1990	1989	-	-	U	U	N	N	N
Patagonian toothfish	1989	-	1991	-	1995	H	N	Y	N	N
Lantern fish	1980s	2003	1992	-	-	U	U	Y	Y	Y
Antarctic krill	1962	-	1992	-	2013	U	U	-	Y	Y

Notation: TAC – year total allowable catch was implemented; H – Heavy, S – Sustainable; U – Unknown; ss – Species specific; Y – Yes; N – No.

Figure 1. A history of population change in marine predators at South Georgia. Dashed line denotes periods of human exploitation; italic font denotes periods of unknown rates of population change; end of available data shown with double line; stacking order is insignificant. source: Boyd (1993); Boyd *et al.* (1996); Clapham *et al.* (1999); Reid and Croxall (2001); Agnew (2004); Trathan *et al.* (2012); Forcada and Hoffman (2014); Chapter 5.



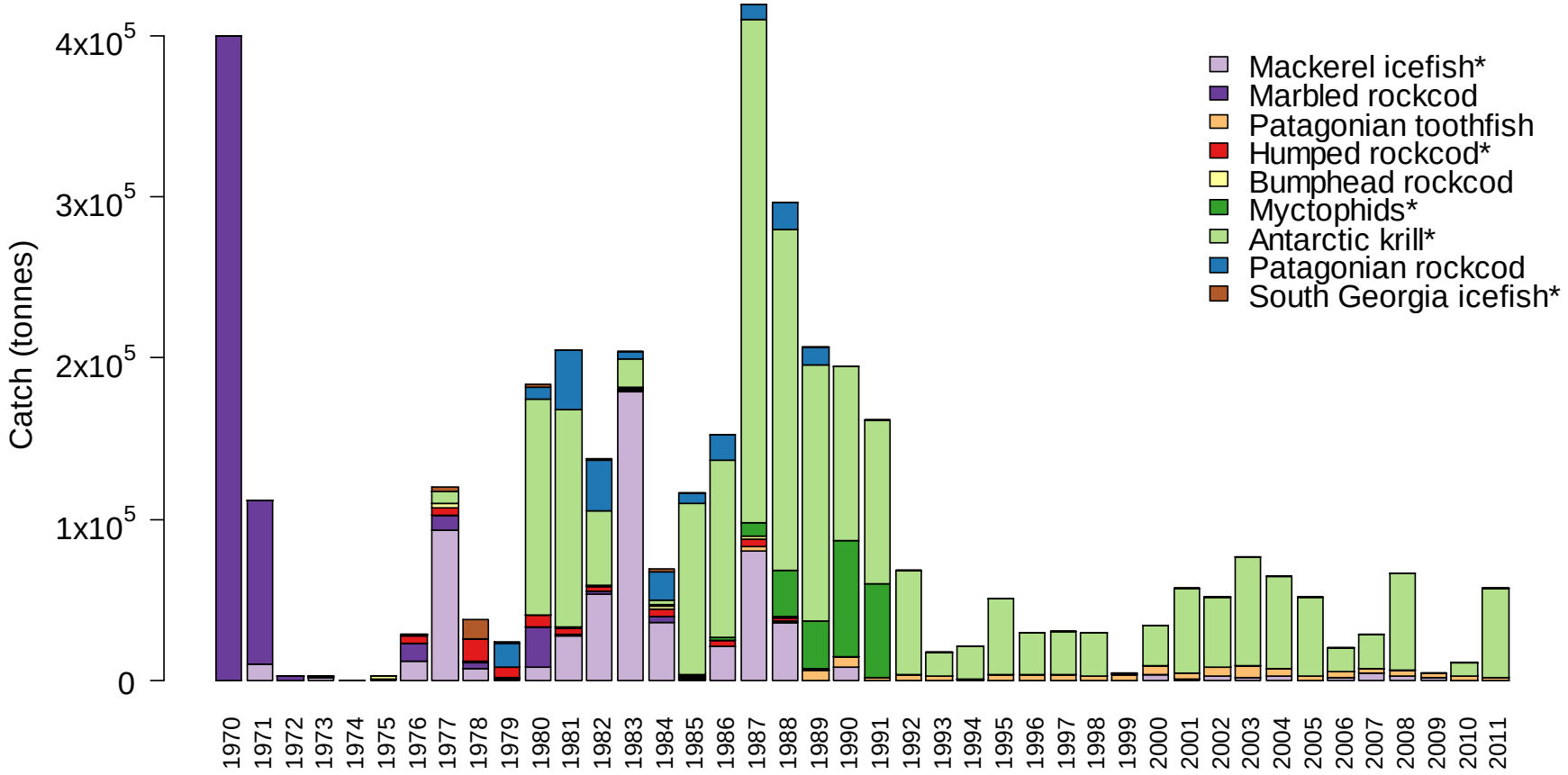


Figure 2. Catch (tonnes) by selected species and fishing season in Subarea 48.3 (South Georgia) (source: Agnew 2004; CCAMLR 2013). * denotes species known to be targeted by macaroni penguins or Antarctic fur seals between 1989 and 2010.

Chapter 3

Survival in macaroni penguins and the relative importance of different drivers; individual traits, predation pressure and environmental variability

This chapter is also published in Horswill, C., Matthiopoulos, J., Green, J. A., Meredith, M. P., Forcada, J., Peat, H., Preston, M., Trathan, P. N. and Ratcliffe, N. 2014. Survival in macaroni penguins and the relative importance of different drivers: individual traits, predation pressure and environmental variability. *Journal of Animal Ecology*, **83**, 1057-1067. DOI: 10.1111/1365-2656.12229 (Accompanying material).

Abstract

Understanding the demographic response of free-living animal populations to different drivers is the first step toward reliable prediction of population trends. Penguins have exhibited dramatic declines in population size, and many studies have linked this to bottom-up processes altering the abundance of prey species. The effects of individual traits have been considered to a lesser extent and top-down processes, such as predation, have been largely overlooked due to the difficulties in empirically measuring this at sea where it usually occurs. For 10 years (2003-2012), macaroni penguins (*Eudyptes chrysolophus*) were marked with subcutaneous electronic transponder-tags, and re-encountered using an automated gateway system fitted at the entrance to the colony. We used multi-state mark-recapture modelling to identify the different drivers influencing survival rates and a sensitivity analysis to assess their relative importance across different life stages. Survival rates were low and variable during the fledging year (mean=0.33), increasing to much higher levels from age 1 onwards (mean=0.89). We show that survival of macaroni penguins is driven by a combination of individual quality, top-down predation pressure and

bottom-up environmental forces. The relative importance of these covariates was age-specific. During the fledging year, survival rates were most sensitive to top-down predation pressure, followed by individual fledging mass, and finally bottom-up environmental effects. In contrast, birds older than 1 year showed a similar response to bottom-up environmental effects and top-down predation pressure. We infer from our results that macaroni penguins will most likely be negatively impacted by an increase in the local population size of giant petrels. Furthermore, this population is, at least in the short-term, likely to be positively influenced by local warming. More broadly our results highlight the importance of considering multiple causal effects across different life-stages when examining the survival rates of seabirds.

Introduction

Understanding the factors that explain changes in population size is central to population ecology, wildlife management and conservation biology. The trajectory of all living populations is determined by several demographic processes, and fluctuations in any one of these can affect the speed with which a population grows or declines. The regulatory mechanisms underpinning these processes are often complex and dynamic, and whilst many studies spanning many species have identified different drivers, few have assessed intrinsic factors, bottom-up and top-down mechanisms simultaneously to provide an insight into their relative importance (see Reid *et al.* 2013). Even fewer have investigated how these effects, when considered in unison, may vary between different life-history stages (see Schwarz *et al.* 2013).

There are many studies suggesting that oceanic predators experience bottom-up control of survival rates where the proposed mechanism is an effect of environmental variability on food availability. For seabirds, these relationships have been inferred for several species (Jenouvrier 2013). The methodological challenges of observing seabirds across large spatial scales and through unobservable life stages (e.g. deferred reproduction) have meant that top-down effects and early life stages have been largely precluded from these studies (Baum and Worm 2009). This is despite predation of seabirds being widely implicated as a potential driver of their population trends (e.g. Andersson 1976; Reisinger *et al.* 2011), and a growing body of literature highlighting that sub-adult life stages play a key role in shaping their population dynamics (Nur and Sydeman 1999; Harris *et al.* 2007; Gaston and Descamps 2011).

Macaroni penguins (*Eudyptes chrysolophus*) are well-studied and have exhibited dramatic declines in population size (Borboroglu and Boersma 2013). Furthermore, they are one of the most important avian marine consumers in the sub-Antarctic region, reported to consume more prey than any other seabird species (de Brooke 2004). Previous studies on this species have linked environmental covariates with the short-term population trajectory, where the proposed mechanism is an effect on reproductive performance (Reid and Croxall 2001; Forcada and Trathan 2009). However, little is currently known about how bottom-up processes influence their survival rates, or what role individual traits and top-down processes, such as predation, have to play. This is despite macaroni penguins appearing as a major component of the breeding season diet for other marine predators (Bonner and Hunter 1982; Hunter and Brooke 1992). Here, we provide the first robust estimates of age-specific survival rates in macaroni penguins. Our analysis avoids the biases associated with flipper banding (Saraux *et al.* 2011a) and is the first seabird demography study to use mark–recapture modelling approaches to simultaneously consider and demonstrate the influence of individual traits, bottom-up and top-down processes.

Methods

Demographic data

For 10 consecutive breeding seasons between 2003 and 2012 (2003 refers to the breeding season spanning November 2002 to April 2003, and so on), adult and fledgling macaroni penguins at Bird Island, South Georgia, were implanted with sterile 32-mm passive integrated transponder (PIT) tags (Texas Instruments, USA). PIT tags were implanted under the skin half way down the back (see Appendix S1 for annual sample sizes in relation to population size and productivity). Within each year, all chicks were PIT-tagged on a single day (16–19th February) shortly before synchronous fledging during mid- to late February. Chicks were selected from the periphery of the crèche; at this stage in the breeding season chicks abandon their individual nest sites during the day in order to 'crèche' together. Because the crèche is highly dynamic (especially in response to disturbance), and the sample of chicks tagged was proportionally large in comparison to the number raised to fledging, the sample was considered to be representative of the whole colony (Appendix S1). In order to minimize disturbance, adults were PIT-tagged periodically throughout the breeding season by capturing them as they entered the colony.

As macaroni penguins are entirely pelagic during the winter months and forage away from the continental shelf zone of South Georgia (Ratcliffe *et al.* 2014), survival rates were

inferred by 'recapturing' individuals during the breeding period. Birds were recaptured using an automated gateway PIT reader system, as described by Green *et al.* (2006). The gateway houses two antennae that electromagnetically activate the PIT tags, scan the unique identifier and store the data to memory. The gateway is situated at the single entrance to the colony, and independent tests have shown reliable recording of individual presence when operational (Green *et al.* 2006). Data from manual recapture using hand-held PIT scanners were also included for all seasons; however, these data were a by-product of studies with aims other than estimating survival rates and therefore were not conducted across the entire colony. Gateway operation was variable between years, and during 2007, the gateway failed completely so that all recaptures were made manually (Appendix S1).

Covariates

To enable a direct comparison of covariate effect size from their regression coefficients, each variable was standardized to $\bar{x} = 0$ and $\sigma = 1$ (Schielzeth 2010).

Individual traits

To examine the within-year effect of individual traits on survival, we used individual body mass at PIT tagging as a proxy for mass at fledging. Macaroni penguins are highly synchronous in their breeding behaviour therefore all the chicks were at a similar age when weighed. Consequently, body mass is also considered to reflect body size. All birds were weighed to the nearest 0.05 kg using a Pesola spring balance. These data were included in the capture histories for birds tagged as chicks. The between-year effect of fledging mass was examined using the annual mean as a time dependent covariate. The year-to-year variation in observed fledging mass was examined using an analysis of variance (ANOVA) model performed in the program R (v. 2.15.3).

Top-down

Northern (*Macronectes halli*) and southern (*M. giganteus*) giant petrels are large birds that are predators and scavengers. At several locations penguins form a major component of their breeding season diet (Bonner and Hunter 1982; Hunter and Brooke 1992). At Bird Island, this is thought to consist predominantly of adult macaroni penguins (Hunter 1983). More recently, anecdotal accounts from Bird Island also report macaroni penguin chicks being heavily predated by giant petrels as they fledge (J. A. Green; P. N. Trathan, pers. obs.; R. A. Phillips, pers. comm.). Reports detail chicks being drowned at sea shortly after

they enter the water, as well as being attacked on land whilst transiting from the colony to the shore. This behaviour is consistent with reports for other penguin species, where predation by giant petrels is reported to take place on land and from the water's surface when leaving or approaching the beach (Le Bohec *et al.* 2003; Ryan *et al.* 2008).

On Bird Island, giant petrels breed sympatrically at densities that at the time of publication were among the highest in the world. Nesting pairs in three study areas were visited weekly during the incubation and chick-rearing stages to determine individual breeding success. The number of giant petrel chicks successfully reared to fledging was used as a proxy for giant petrel predation pressure. This measure relates to the number of giant petrels that would still be under central place constraint and therefore foraging locally when the penguin chicks fledge.

Bottom-up

We quantified the effect of one local and two quasi-remote environmental variables: 1. local sea surface temperature anomalies in the region associated with foraging during the breeding season (Figure 3; 35.5°W to 44. 5°W; 52.5°S to 54.5°S) (LSST); 2. the El Niño/Southern Oscillation (ENSO) phenomenon; and 3. the Southern Annular Mode (SAM).

This population of macaroni penguins have an extensive latitudinal and longitudinal dispersal during the winter (Ratcliffe *et al.* 2014). To minimise the signal being masked by the large variation in SST across the large winter range, we used the average SST associated with the foraging range during the breeding season (Figure 3). LSST is used here as a proxy for the diverse processes that are thought to influence prey retention and survival within the continental shelf zone; such as oceanic advection and upwelling (Murphy *et al.* 1998; Trathan *et al.* 2003). Surface warming of the oceans is accompanied by a reduction in productivity (Behrenfeld *et al.* 2006), and has also been linked to a decrease in fish spawning and an increase in their egg mortality (Potts *et al.* 2014). Antarctic krill (an important component of macaroni penguin diet at South Georgia; Waluda *et al.* 2012) are not thought to be self-sustaining in this region, but are exported from spawning grounds and transported to South Georgia via advection (Murphy *et al.* 1998). The Antarctic Peninsula, the South Orkney Islands and the Weddell Sea have all been highlighted as potential source regions (Siegel 2005), although modelling studies also show that oceanic waters right across the Scotia Sea offer suitable conditions for krill

spawning and larval development (Hofmann and Hüsrevoğlu 2003). The large-scale distribution of krill around South Georgia is thus a function of production (recruitment and growth) and dispersal from spawning grounds, as well as retention and mortality in the study region (Murphy *et al.* 2007). We used LSST data calculated according to methods described by Reynolds *et al.* (2002) and obtained from the National Oceanographic and Atmospheric Administration (NOAA) through the International Research Institute. The data are optimum-interpolation LSST values, produced monthly on a one degree grid using in situ and satellite LSST, plus LSST estimated from sea-ice cover. Data are available at http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/.SSTa/.

The remote environmental variables (ENSO and SAM) offer proxies for remote forcing on LSST, in addition to other environmental variables throughout the Southern Ocean (Meredith *et al.* 2005, 2008). ENSO is a major mode of coupled atmosphere ocean variability that operates on inter-annual timescales. Whilst it is triggered in the equatorial/tropical Pacific, it has teleconnections to the Southern Ocean and Antarctica via both atmospheric and oceanic processes (Turner 2004). SAM is the dominant mode of extra-tropical variability in the Southern Hemisphere and is characterized by shifts in atmospheric mass between a node centred over Antarctica and a ring encompassing the lower latitudes. SAM fluctuates on timescales of weeks to decades, including inter-annual periods, and is associated with variations in the circumpolar winds over the Southern Ocean (Sengupta and England 2006). As physical variability in this region is linked with the extent of sea ice during the winter, we used a summer mean of the remote climatic covariates, which corresponds to the breeding season when birds are under strong central place constraints. Whilst teleconnections between LSST, ENSO and SAM at South Georgia mean that these variables are not independent, the relationship is highly dynamic over time, precluding the use of principal component analysis. For ENSO, we used the bivariate ENSO time series (BEST) index (Smith and Sardeshmukh 2000). This is broadly equivalent to the Southern Oscillation Index (SOI), which has been used previously as a proxy for ENSO variability (e.g. Jenouvrier *et al.* 2005). The BEST index offers advantages as it also includes an oceanic component (Niño 3.4 SST index) as opposed to being derived from two atmospheric stations only (Smith and Sardeshmukh 2000). Monthly values of the BEST index were obtained from the Climate Diagnostics Center of NOAA (data available at http://www.cdc.noaa.gov/people/cathy.smith/best/), and monthly

values of the SAM index were obtained from the Climate Prediction Center of NOAA (obtained from http://www.cpc.ncep.noaa.gov/).

Candidate temporal lags were calculated from published information by summing plausible physical and biological process lags (Appendix S2). Whilst a positive phase of the SAM is associated almost immediately with warm LSST anomalies in the study region (at time lags of ~1 month), positive ENSO values generally take 1.5–2 years to appear as warm LSST anomalies in the Scotia Sea (Meredith *et al.* 2008). Biological lags associated with the recruitment of krill to South Georgia were added to the physical lags in two potential spawning and dispersal scenarios. Either spawning occurs across the Scotia Sea with recruitment maintained within that year in all shelf regions (Brierley *et al.* 1999), or spawning and successful survival through the first year occurs mainly in central and southern areas of the Scotia Sea with dispersal occurring through interactions with the ocean and sea ice over the next 1–2 years (Hofmann *et al.* 1998).

Data analysis

Capture–mark–recapture modelling of survival

Construction of individual capture histories was carried out using R and Microsoft Access (Cooch and White 2011). The interval between sampling intervals was 1 year, from the end of the moulting period in year$_t$ to the end of the moulting period in year$_{t+1}$ (1st May of year$_t$ to 30th April of year$_{t+1}$; macaroni penguins renew their feathers at the end of the breeding season). As chicks fledge the colony before the moulting period the survival interval for this age class started slightly earlier; however, survival rates are considered to represent the fledging year interval, also finishing in the subsequent year at the end of moult. Separating survival rates between the breeding and interbreeding season was not considered as part of this study.

The data set contained 966 individuals PIT tagged at age 1 or above and 1070 individuals PIT tagged at fledging (Appendix S1). Any individuals PIT tagged at fledging without mass data were removed from the analysis (n = 11; 7 birds from 2009, 4 birds from 2011). Annual survival rates were estimated using a multistate capture–mark–recapture model fitted using Program MARK (Lebreton and Pradel 2002). Conventional mark-recapture models assume that survival and recapture do not vary between individuals in a group, that no marks are lost, and that the population is a closed system (Lebreton *et al.* 1992). In order to account for the heterogeneity in recapture rates associated with deferred

reproduction, individuals within the population were classified into two states. State 1 included all birds PIT tagged at fledging that have not yet returned to the colony (the 'unobservable state'). State 2 included birds tagged at age 1 or above and birds tagged at fledging that have since returned to the colony and are assumed to be available for recapture on an annual basis (the 'observable state'). This approach simplifies the model structure by allowing individuals to return to the colony for the first time at different ages, as opposed to using complex interactions to describe age-dependent recapture rates (e.g. Spendelow *et al.* 2002).

The starting model (here on referred to as the 'global model') was constructed to have the largest number of parameters that was biologically meaningful to the study system whilst also providing adequate fit to the data. The goodness-of-fit of this model was assessed using the overdispersion parameter, median $\hat{c}$, as this offers the most suitable approach for multistate models with age-specific transitions (Cooch and White 2011). Median $\hat{c}$ was estimated with a lower bound of 1.0, an upper bound of 4.0 and 100 replicates, and a score greater than 3 was taken to represent lack of fit (Lebreton *et al.* 1992). The error of all candidate models was increased by this value during model selection. The global model structure incorporated age-specific variation in transition rates from the unobservable to the observable state; state and time-specific variation in recapture rates; and an interaction between age and time-specific variation in survival rates. All candidate models were nested within this model, and the most parsimonious was selected using the second-order Akaike information criterion (AIC_c) (Burnham and Anderson 2002). A difference of less than 2 AIC_c units was taken to suggest that competing models received a similar amount of support from the data. In this case, the model with greater deviance explained was selected. A difference of more than 2 indicated strong support for the model with the lower AIC_c (Burnham and Anderson 2002).

Transition probability: age of first return to the colony (Ψ)

Age of first return to the colony was modelled with a maximum at 3, 4 and 5 years old. The model thus estimated the probability that if an individual survives until year *t* and age *i*, they will return to the colony for the first time at age *i*, up to the respective maximum age. The probability of birds older than these maxima returning for the first time was fixed to a value of one (Spendelow *et al.* 2002). Since birds entering the observable state are then assumed to be available for recapture on an annual basis, the reverse transition back into a deferred reproduction state was fixed to a value of zero (Spendelow *et al.* 2002). Model

simplification involved fitting age of transition as a linear and natural logarithm trend. This allowed the relationship between age and transition probability to change according to a function, reducing the number of parameters necessary to model this rate from 4 to 2. Incomplete attendance histories at the individual level, caused by variable operation of the gateway PIT reader within seasons, precluded the identification of individual recruitment to the breeding population from seasonal attendance patterns (see Le Bohec *et al.* 2007).

Recapture probability (p)

The recapture probability of birds in the unobservable state was fixed to zero (*p0*). For birds in the observable state, recapture probability was allowed to vary from year to year (p_t). Model simplification involved fitting a reduced time-dependent variable with seasons grouped manually based on the duration the gateway PIT reader was in operation (p_{T3}): 1. not working (0 days: 2007); 2. working intermittently (1–100 days: 2009); and 3. working well (>100 days: all other years) (Appendix S1). A constant recapture probability through time was also tested.

Survival probability (ϕ)

Survival was modelled with three separate age classes (*a3*: fledging year, second year and all years thereafter), two separate age classes (*a2*: fledging year and all years thereafter) and without age effects (*a1*). The effect of age and time was tested as additive and interactive with age class. After selecting the best age structure, the yearly variation in survival probabilities was modelled as an age-specific function of individual- and year-specific covariates using a step-up approach. The influence of individual traits (fledging mass; for birds marked as chicks only) was tested in isolation using a likelihood ratio test (LRT; Skalski *et al.* 1993). Each year-specific covariate was then fitted alongside individual fledging mass and the most significant retained. This process was iterated until the addition of any remaining year-specific covariates did not significantly improve the amount of deviance explained by the model. The proportion of deviance accounted for by the inclusion of each additional covariate (R^2_DEV) was calculated as [DEV(Model.) - DEV($Model_{cov}$)/DEV(Model.) - DEV($Model_t$)], where DEV was the deviance for models with constant (.), covariate (cov) and total temporal (t) variation (Skalski *et al.* 1993). The model including the covariate selected during the previous step was used as the constant model. A covariate explaining more than 20% of the remaining deviance was taken to be significantly influential (Grosbois *et al.* 2008). The statistical support for a covariate effect was also measured using ANODEV in Program MARK (Skalski *et al.* 1993). Finally, the

significance of each covariate retained by the best candidate model was verified through the confidence interval of its logit-scale regression coefficient. Variance component analysis was used to assess the total time-dependent process variation (σ) in the survival rates of each age class (Cooch and White 2011).

Sensitivity analysis

To assess the relative importance of each covariate within the best candidate model, we compared covariate effect sizes and calculated the partial derivative of survival with respect to each variable in a sensitivity analysis. For example, in a model where fledgling mass (*Mass*) is the only explanatory variable retained, the sensitivity (*S*) of survival (ϕ) to mass would be calculated as:

$$S_{Mass} = \frac{\partial \bar{\phi}}{\partial \overline{Mass}} = \hat{\beta}_1 \left(\hat{\phi} - \hat{\phi}^2 \right)$$

where $\text{logit}(\phi) = \beta_0 + \beta_1 Mass$.

Results

The global model

For the global model with three age classes and maximum age of transition at 5 years old, median $\hat{c}$ was estimated at 2.96 (SE = 0.02) (Table 2: model 8) (see Table 2 and Appendix S3 for all other candidate models). The addition of further age classes within the global model structure led to a substantial loss of fit (median $\hat{c} > 3$).

Age of first return to the colony

Virtually all birds had transited to the observable state by age 4 years (Table 2: model 6 vs. 5, 7, Figure 4, Appendix S3). The overall trend for rate of first return was best described by a natural logarithm function (Table 2: model 3 vs. 4, 6, Figure 4). The rate of birds returning to the colony by age 1 was low (0.1; 10% of the population), increasing dramatically so that cumulatively 89% had returned by age 3 (Figure 4).

Factors affecting recapture rates

There was high variability in the annual recapture probability of observable birds (Table 2: model 3 vs. 10). This was best explained by the annual variation in the number of days that the gateway PIT reader was operational (Table 2: model 2 vs. 3). Recapture rates were

predominantly high when the gateway was in operation for more than 100 days (0.99); slightly reduced during years with intermittent operation (0.88); and considerably lower when reliant on manual recaptures only (0.15).

Factors affecting survival rates

The annual variation in survival rates was best described in two age classes (Table 2: model 5 vs. 8–9, Appendix S3), and the difference between these was additive with time (Table 2: model 1 vs. 2). Survival rates were considerably lower and more variable during the fledging year (Figure 5; $\bar{x}$ = 0.33, SE = 0.06, σ = 0.12) than in the older age class (Figure 5; $\bar{x}$ = 0.89, SE = 0.01, σ = 0.01). Due to large confidence intervals associated with the proportion of birds still in the unobservable state, the fledgling age class for 2010 is not presented.

The step-up procedure produced three significant variables influencing survival rates during the fledging year and two significant variables influencing the survival rates of birds older than 1 year; the results of this procedure are summarized in Table 3 (see Appendix S4 for all other candidate models and Appendix S5 for parameter estimates). Within a year, heavier chicks had consistently higher rates of survival than lighter ones so that the slope of this relationship is the same across years (Table 3, Figure 6). However, the intercept term of this relationship was not adequately described by the inter-annual variation observed in fledging masses (Figure 6: $\bar{x}$ = 3.28; ANOVA: $F_{7,814} = 38.73$, $P < 0.001$). For example, during 2009 considerably lower fledging masses and survival rates were documented, but during 2005 and 2008 low-to-average survival rates were documented despite fledging masses being average to high (Table 3, Figure 6).

The step-up procedure showed the year-to-year variation in survival rates of both age classes to be best described as a function of predation pressure and $LSST_{-1}$ (Table 3). Although the interaction between predation pressure and age class was at the boundary of influence, this parameter was retained as anecdotal evidence reports a considerably higher incidence of giant petrel predation on fledgling chicks compared with adults (J. A. Green; P.N. Trathan, pers. obs.). Both age classes showed a negative response to predation pressure that was smaller in the older age class (Table 4, Figure 7; Appendix S5). Bottom-up control from $LSST_{-1}$ was best incorporated as an additive effect that was positive for both age classes (Table 4; Appendix S5). There was no evidence for any additional effects from $LSST_0$, $ENSO_{-2}$, $ENSO_{-3}$, SAM_0 or SAM_{-1} (Appendix S4: R^2_DEV<0.2, $P > 0.05$).

Survival rates during the fledging year were most sensitive to top-down predation pressure, followed by individual fledging mass, and finally bottom-up environmental effects (Table 4). In contrast, the older age class showed a similar response to fluctuations in bottom-up processes and top-down predation pressure (Table 4). Consistent with the lower variance, the strength of these effects was much smaller on the older age class (Table 4).

Discussion

Age of first return to the colony

Despite operation of the automated gateway PIT reader being variable between years, this study obtained high detection rates when the gateway was functioning. This system is therefore highly suitable for estimating annual survival rates during deferred reproduction. The brief colony attendance of immature penguins means that conventional visual observation methods are likely to overestimate the age of first return. We found that more than 75% of immature birds had returned to the colony for the first time by age 3 and that 10% visited the colony in their first year. Based on surveys of banded birds, first breeding attempts of macaroni penguins are not thought to occur until age 6–8 (Williams 1995). However, other studies based on banded crested penguins have shown that first return to the breeding site coincides with age of first reproduction attempt (±1 year; Guinard *et al.* 1998). As macaroni penguins may reach physiological maturity several years in advance of first breeding attempts (Williams 1992), further work is needed to define the mean age of recruitment for this population. An explanation for birds returning earlier in life is to start prospecting future breeding sites (Boulinier *et al.* 1996).

Factors affecting survival

Age

The survival rates of macaroni penguins were best described in a two age class structure. Birds experienced low and variable survival rates during the first year following fledging, and higher, more stable survival rates from age 1 onwards. Whilst it is not uncommon for seabirds to experience lower rates of survival during the fledging year (e.g. Frederiksen *et al.* 2008), other PIT-tagged penguins that breed in sub-Antarctica have shown fledgling survival rates to be more similar to birds older than 1 year (king penguins *Aptenodytes patagonicus*, Saraux *et al.* 2011b). The rates reported here are more similar to species that predominately breed in temperate zones, such as those reported for PIT-tagged little penguins (*Eudyptula minor*; 0.05–0.60: Sidhu *et al.* 2012) and banded northern rockhopper penguins (*Eudyptes moseleyi*; 0.27: Guinard *et al.* 1998). Given the large variation between

our seven study cohorts of fledgling birds (2003–2009), with rates almost comparable with the older cohort during 2003, it is possible that given certain extrinsic conditions (i.e. a low predation pressure and an elevated $LSST_{-1}$), fledgling macaroni penguins are capable of much higher levels of survival. Further investigation into the distribution of immature penguins is needed in order to compare immature survival rates between species. During the inter-breeding season, adult macaroni penguins remain further north (Ratcliffe et al. 2014) than king penguins (Charrassin *et al.* 2001; Bost *et al.* 2004). The elevated immature survival rates of king penguins (Saraux *et al.* 2011b) may indicate that the availability of their target prey species is more reliable during winter. An alternative explanation is differing levels of natal dispersal. Dispersal of penguins is still studied almost exclusively using flipper bands (e.g. Reilly and Cullen 1982) that can impair survival rates (Saraux *et al.* 2011a). Therefore, reported rates for natal dispersal may not be representative of actual population dispersal and may constitute a bias (Saraux *et al.* 2011a). Consequently, post-hoc adjustment of immature return rates in order to account for natal dispersal was avoided. The rates we report for the older age class correspond with those reported for other penguin species that breed in the sub-Antarctic region and are marked with PIT tags (0.82–0.96; Le Bohec *et al.* 2008; Dehnhard *et al.* 2013).

Individual traits

Within a given year, macaroni penguins fledging with heavier body masses consistently showed higher survival rates than birds fledging lighter. This agrees with previous work on penguin species marked with flipper bands (Olsson 1997; McClung *et al.* 2004). Given the detrimental effects of flipper banding (Saraux *et al.* 2011a), the consistency of this correlation in our study population (that are marked with PIT tags) further affirms that within a given year fledging penguins are highly dependent on their somatic resource whilst they gain the necessary foraging experience to search for patchily distributed prey (see also Saraux *et al.* 2011b).

Fledging mass of macaroni penguins is a function of growth rates driven by parent bird foraging and provisioning strategies (Barlow and Croxall 2002b). Both fledging mass and survival rates were lower than average during 2004 and 2009, which coincides with years when macaroni penguin diet switched from being predominantly krill, to predominantly fish or *Themisto gaudichaudii* (Waluda *et al.* 2012). In addition, during 2004 parent birds from our study site were foraging further afield; an indication that they were targeting a different prey source (Trathan *et al.* 2006). A change in food supply is thus the most

obvious explanation for the low masses observed during 2004 and 2009. However, the lack of a year-to-year relationship between fledging mass and survival indicates that this variable cannot be the only driver affecting the survival rates of this age class. Furthermore, as the individual fledging mass covariate remains significant in a model that also includes a bottom-up covariate, where the proposed mechanism incorporates food supply, we suggest that intrinsic traits such as structural size and physiology are also important when assessing individual quality.

Top-down effects

This is one of the first studies to illustrate how penguin survival rates may change under different levels of predation pressure from giant petrels. Predation pressure was shown to have a significant negative effect on both fledgling and adult macaroni penguins, albeit to a much lesser extent in adults. Lacking in experience, size and strength, fledgling birds are more susceptible to predation, and of the covariates considered, predation pressure had the strongest impact on survival during the fledging year. This was particularly apparent during 2005 and 2008, when average-to-high fledging masses and average environmental conditions coincided with elevated levels of predation pressure to produce lower-than-average survival rates.

Giant petrels are known to kill prey of similar and greater mass than an adult macaroni penguin (Le Bohec *et al.* 2003), and our results support anecdotal observations of direct predation (J. A. Green; P. N. Trathan, pers. obs.; R. A. Phillips, pers. comm.). Furthermore, this study corresponds with dietary analysis that shows macaroni penguins form a major component of giant petrel diet during the breeding season (Hunter 1983). Further work is needed to understand how giant petrels utilize different on-land prey resources (i.e. fur seal carcasses, penguins; Bonner and Hunter 1982; Hunter and Brooke 1992; González-Solís *et al.* 2000). Whilst giant petrels show species- and gender-driven segregation of foraging areas (González-Solís *et al.* 2000), it is unknown how this translates onshore during times of elevated resource, such as the synchronized fledging of penguin chicks. Under the observed conditions, we can predict that macaroni penguins are likely to be negatively affected by an increase in the population size of giant petrels, although the possibility of interference competition should be considered when making long-term projections. Finally, our study focuses on near-shore predation effects associated with the local giant petrel population. However, offshore predation by these and other species cannot be discounted despite being harder to empirically observe. There are near-shore observations

of killer whales (*Orcinus orca*; Pitman and Durban 2010), leopard seals (*Hydrurga leptonyx*; Ainley *et al.* 2005) and otariid species (Bonner and Hunter 1982; Lalas *et al.* 2007) predating on various species of penguin, yet little is known about how these predators may influence survival rates during both the breeding and interbreeding period.

Bottom-up effects

Climatic change can have contrasting effects on different penguin populations and species (Croxall *et al.* 2002). We infer from our results that macaroni penguin survival at South Georgia has a positive association with local warming. Whilst the majority of penguin climate demography studies report a negative association between climate warming and the survival rates of adult penguins (Barbraud and Weimerskirch 2001; Le Bohec *et al.* 2008), a positive effect has also been noted in specific populations of temperate and sub-Antarctic fledgling birds (Saraux *et al.* 2011b; Sidhu *et al.* 2012). It should also be kept in mind that $LSST_{-1}$ does not necessarily drive survival rates to change; rather $LSST_{-1}$ represents local environmental conditions and physical variability. Thus, each species could have optimum extrinsic conditions such that relationships between survival and environmental effects are nonlinear and possibly non-monotonic. The observed trend with warming will thus depend on whether the conditions at the study location are above or below the optimum (see Croxall *et al.* 2002; Jenouvrier *et al.* 2012). Due to the positive relationship shown here, we suggest that the range of LSST values observed during the study period represents below optimum conditions for macaroni penguin survival. Determination of the point at which environmental conditions move across the optimum threshold would require a longer time series with greater variation in LSST.

It is also possible that $LSST_{-1}$ is acting as a proxy for a separate process. This could be a remote effect associated with krill dispersal from the spawning ground, or a more local effect at South Georgia associated with krill retention and survival throughout the year. Atkinson *et al.* (2004) show a correlation between decreased levels of krill in the study area and reduced winter sea-ice extent further south. Here the proposed mechanism is a depletion of winter resources at the spawning grounds. In contrast, Loeb *et al.* (1997) show years of extensive sea ice increasing the retention of krill at the spawning ground, which may decrease the biomass of krill further upstream in the study area. Enhanced krill recruitment to South Georgia is therefore most likely to be associated with winters of average ice conditions (Quetin and Ross 2003). In terms of a local effect, conditions at South Georgia may control the proportion of krill that survive and are retained throughout

the year. Despite krill density in these waters being lower during the winter months, concentrations are still substantial enough to support a seasonal fishery within the continental shelf zone (Trathan *et al.* 1998). Year-round local conditions are therefore likely to influence the biomass of the basal prey stock from one breeding season to the next (Murphy *et al.* 1998). Further work is needed to elucidate how local environmental conditions affect the resident prey species at South Georgia.

During the breeding season, the main foraging ground of macaroni penguins from Bird Island overlap with the foraging grounds of Antarctic fur seals. The rapid recovery of fur seals following the cessation of their commercial exploitation (Trathan *et al.* 2012) means they are now considered to be a major competitor for krill during the breeding season (Reid *et al.* 1996).Whilst we do not examine the effects of interspecific competition in this study, growth of the fur seal population at Bird Island stabilized and started declining prior to the study period examined here (1985–2000; Reid and Croxall 2001). Furthermore, as the winter foraging areas of these species are largely different (Staniland *et al.* 2012; Ratcliffe *et al.* 2014), increased levels of interspecific competition during the breeding season are more likely to affect population productivity as opposed to survival rates.

Conclusion

This study represents the first seabird demography study to use mark–recapture modelling approaches to simultaneously consider and demonstrate the influence of individual traits, top-down and bottom-up processes. We show that inter-annual variation in survival rates of macaroni penguins at South Georgia is forced by a combination of fledging mass, predation pressure and environmental variability. Under the observed conditions, we can predict that, at least in the short term, macaroni penguins will most likely be negatively affected by an increase in the population size of giant petrels and positively affected by local warming. Despite marked uncertainty in the long-term behaviour of the environmental variables considered, most IPCC class models predict continued warming in the Southern Ocean over the coming decades. We show that fledging macaroni penguins are most sensitive to fluctuations in top-down predation pressure, followed by the effects of fledging mass and then bottom-up control. In contrast, birds older than 1 year have a similar response to fluctuations in bottom-up processes and top-down predation pressure. The age-specific response of macaroni penguins to the physical and biological processes considered here confirms the importance of considering multiple causal effects across multiple life stages when examining the survival rates of seabirds.

Table 2. Modelling capture, survival and transition probabilities for macaroni penguins breeding on Bird Island, South Georgia (2003-2012).

No.	Model	$QAIC_c$	$\Delta QAIC_c$	k	QModel deviance
1	$\phi_{a2\,a+t/a+t}\ p_{0/T3}\ \Psi_{4\,ln\,/0}$	1816.37	0.00	18	1786.27
2	$\phi_{\ a2\,a*t/a*t}\ p_{0/T3}\ \Psi_{4\,ln\,/0}$	1817.77	1.4	26	1769.53
3	$\phi_{a2\,a*t/a*t}\ p_{0/t}\ \Psi_{4\,ln\,/0}$	1817.81	1.44	31	1767.55
4	$\phi_{a2\,a*t/a*t}\ p_{0/t}\ \Psi_{4\,linear\,/0}$	1820.72	4.35	31	1770.46
5	$\phi_{a2\,a*t/a*t}\ p_{0/t}\ \Psi_{5/0}$	1821.28	4.91	34	1762.94
6	$\phi_{\ a2\,a*t/a*t}\ p_{0/t}\ \Psi_{4/0}$	1823.01	6.64	33	1766.69
7	$\phi_{a2\,a*t/a*t}\ p_{0/t}\ \Psi_{3/0}$	1843.22	26.85	32	1790.95
8	$\phi_{a3\,a*t/a*t}\ p_{0/t}\ \Psi_{5/0}$	1872.68	56.31	42	1814.34
9	$\phi_{a1\,t}\ p_{0/t}\ \Psi_{5/0}$	1931.00	114.63	25	1890.83
10	$\phi_{a2\,a*t/a*t}\ p_{0/.}\ \Psi_{4\,ln\,/0}$	2411.78	595.41	23	2373.63

Notes; Model fit is assessed using the lowest $QAIC_c$ with the difference between the best candidate model and other models specified ($\Delta QAIC_c$). See Appendix S3 for global models considered for age classes and maximum age of transition. Here, k is the number of parameters in the statistical model. Explanation of model notation (Cooch & White 2011): (ϕ) refers to the structure used to model survival probabilities, (p) refers to capture probabilities, and (Ψ) refers to transition probabilities. p and Ψ probabilities are separated by a forward slash to show the model structure for each state, unobservable/observable; / probabilities are separated by a forward slash to show the model structure for each age class, fledgling year/older than 1 year. (a) shows whether the function refers to a 1, 2 or 3 age class structure. (t) indicates a fully time-dependent structure; ($a*t$ or $a + t$) a fully time-dependent structure that is interactive or additive with age; (.) a constant structure; and (0) a fixed probability at zero.

Table 3. Step-up model selection procedure, ANODEV and LRT tests for examining the influence of individual trait, top-down and bottom-up covariates on the survival rates of macaroni penguins. At each step only the most significant variable is shown. Recapture and transition probabilities specified as Model 1 (Table 2).

Step	Model	k	*df*	ANODEV tests for cohort-level covariates			LRT tests for individual-level covariates	
				F	*P*	R^2	χ^2	*P*
1	. / .	10	-	-	-	-	-	-
2	Mass / .	11	1	-	-	-	11.00	<0.01
3	Mass + Pred. / Pred. *	12	1	11.29	<0.01	0.43	-	-
4	Mass + Pred. / Pred.	13	1	3.46	0.08	0.20	-	-
5	Mass + Pred. + $LSST_{-1}$ / Pred. + $LSST_{-1}$	14	1	7.25	0.02	0.36	-	-
6	Mass + Pred. + $LSST_{-1}$ + SAM_0 / Pred. + $LSST_{-1}$ + SAM_0	15	1	1.46	0.22	0.12 n.s. Stop	- »	-

Notes; Survival probabilities are separated by a forward slash to show the model structure for each age class, fledgling year/older than 1 year. Unless specified predation pressure was included as an interactive effect with age class and environmental covariates as an additive effect with age class (see Appendix S4 for all other candidate models considered). (*) Predation pressure included as an additive effect with age class. (*df*) degrees of freedom given as the difference in the number of estimable parameters between the two models compared using the step-up procedure. R^2 (R^2_DEV) gives the further deviance explained by adding a covariate.

Table 4. The relative importance of each covariate to modelling the year-to-year variability in survival rates of macaroni penguins breeding on Bird Island, South Georgia.

Age Class	Covariates		
	Fledging mass	Predation Pressure	$LSST_{-1}$
Fledgling	0.09	-0.15	0.03
>1 yr. old	-	-0.02	0.01

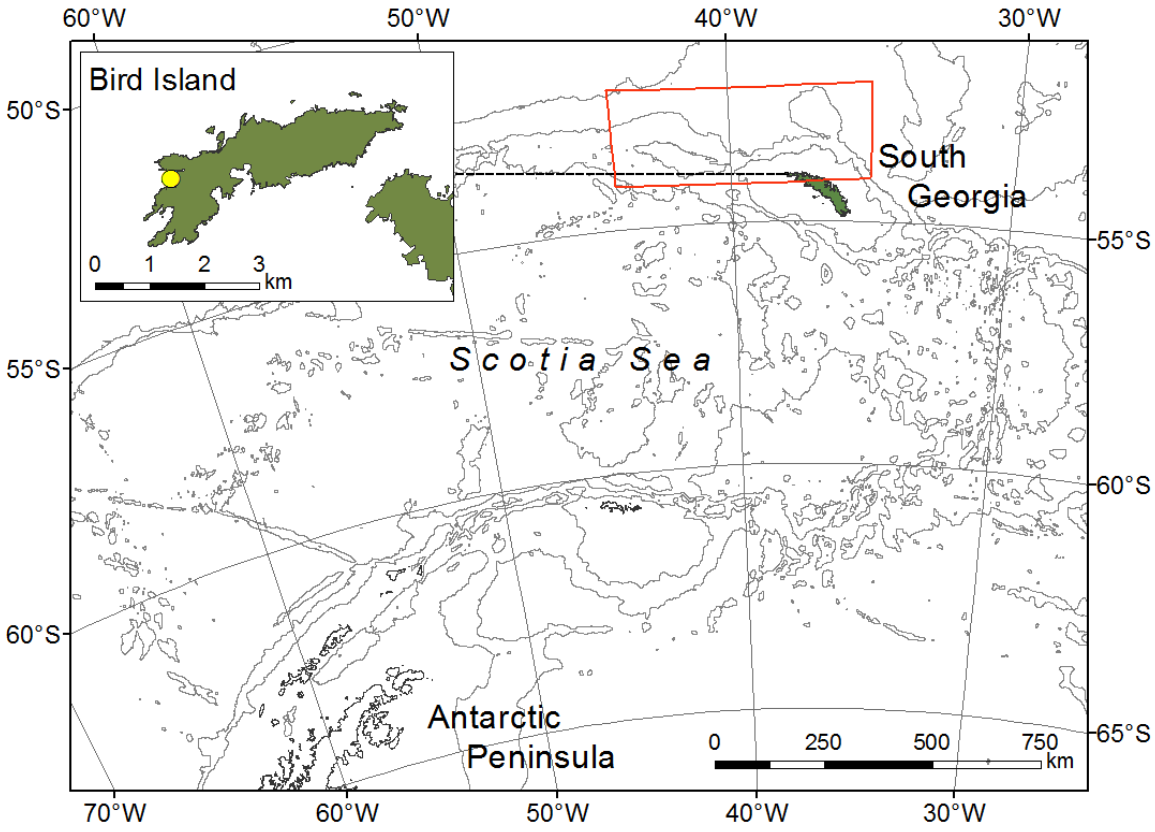


Figure 3. Map of Bird Island in relation to the Antarctic Peninsula. Bird Island with study colony shown within the insert map, dashed line to location at South Georgia. Bathymetry contours at 1000m, 3000m, 5000m. Spatial scale of LSST covariate shown by red square.

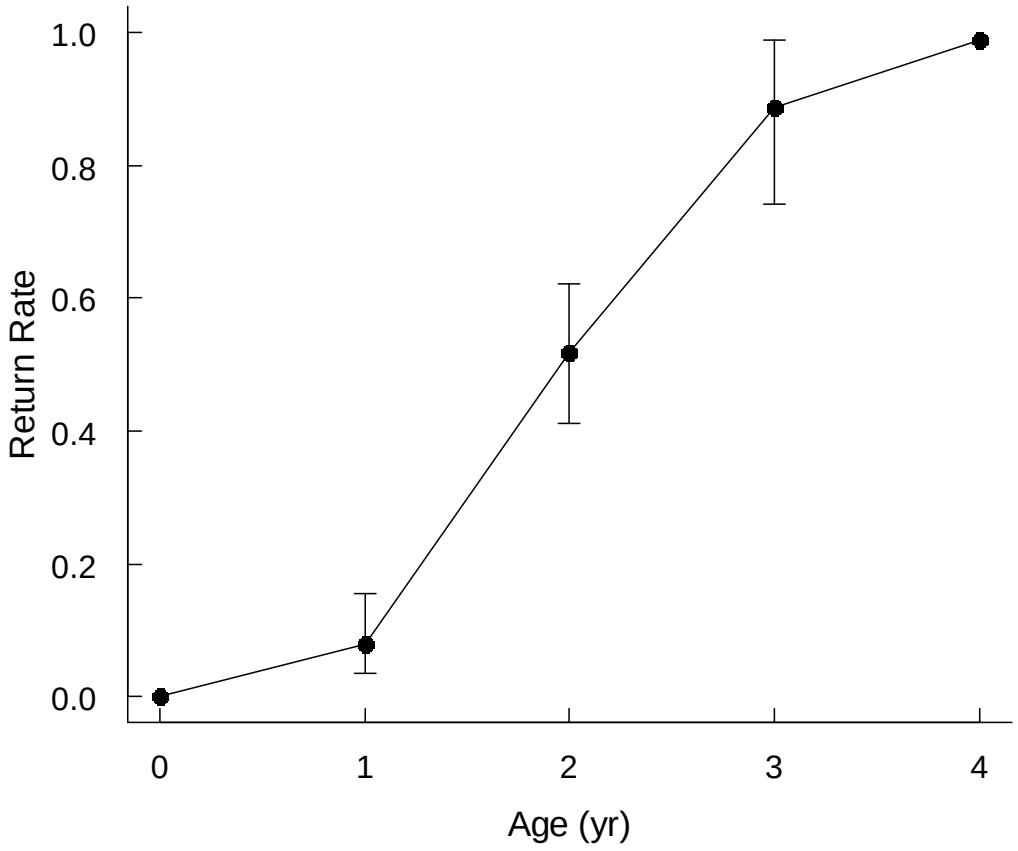


Figure 4. Cumulative rate of first return to the colony at different ages (as a natural logarithm function with 95% confidence intervals).

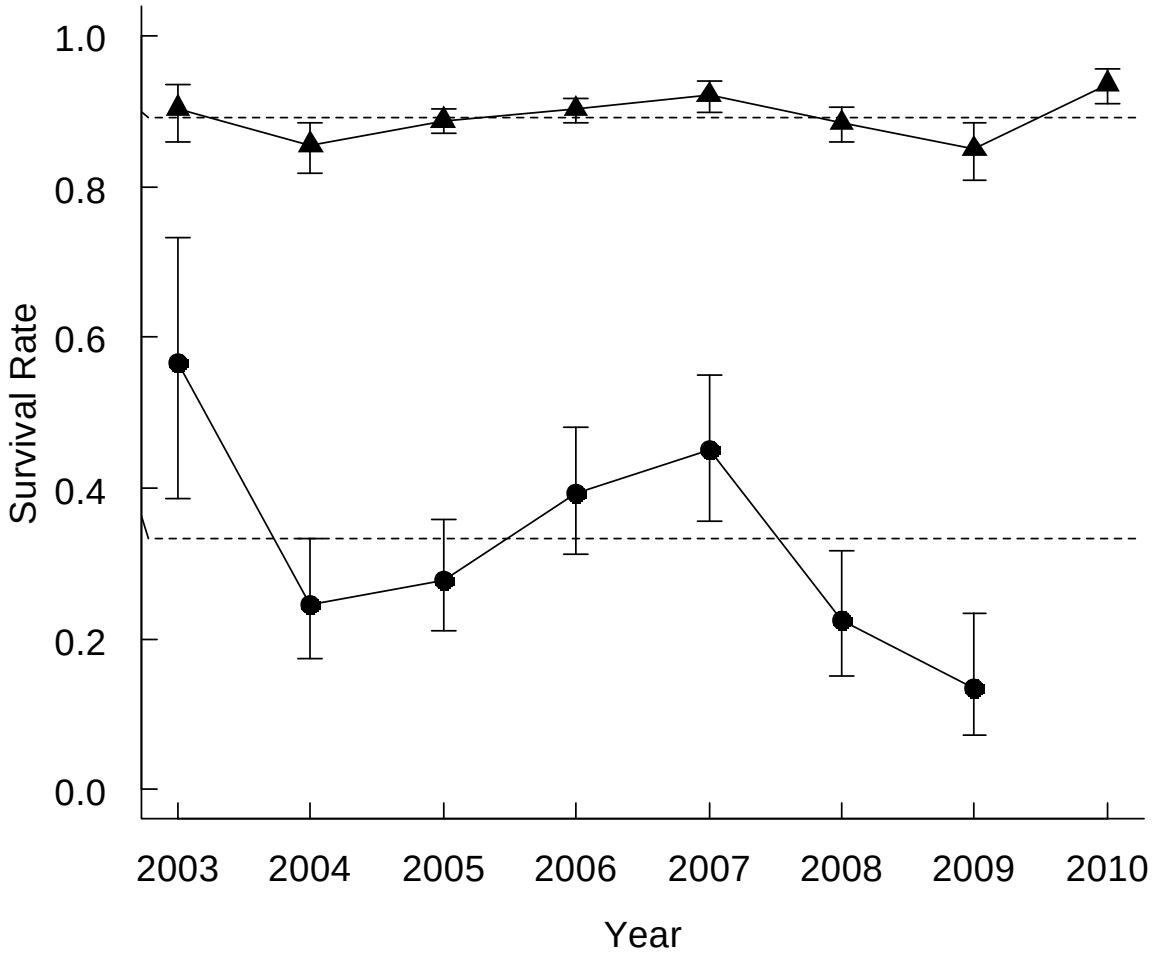


Figure 5. Survival rates of macaroni penguins breeding on Bird Island, South Georgia, by age class. Fledging year (black circles) and birds older than 1 yr. (black triangles). Age specific means are shown with dashed lines.

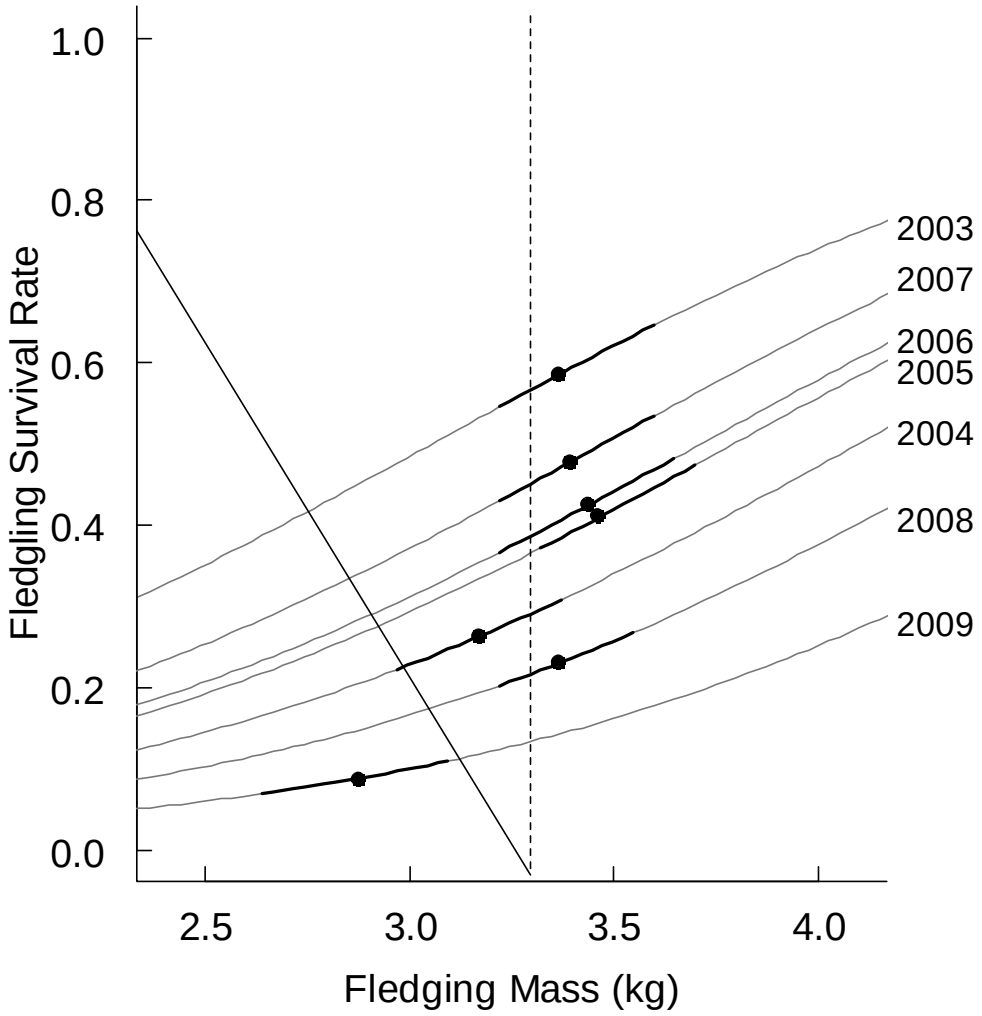


Figure 6. The survival rate of fledgling macaroni penguins modelled as a function of fledging body mass. The annual inter-quartile range (black line), annual mean (black circles), and overall mean (dashed line) shown for observed masses. Extrapolation of fledgling survival rate over a range of de-standardized values for fledgling mass (grey line) was carried out within Program MARK.

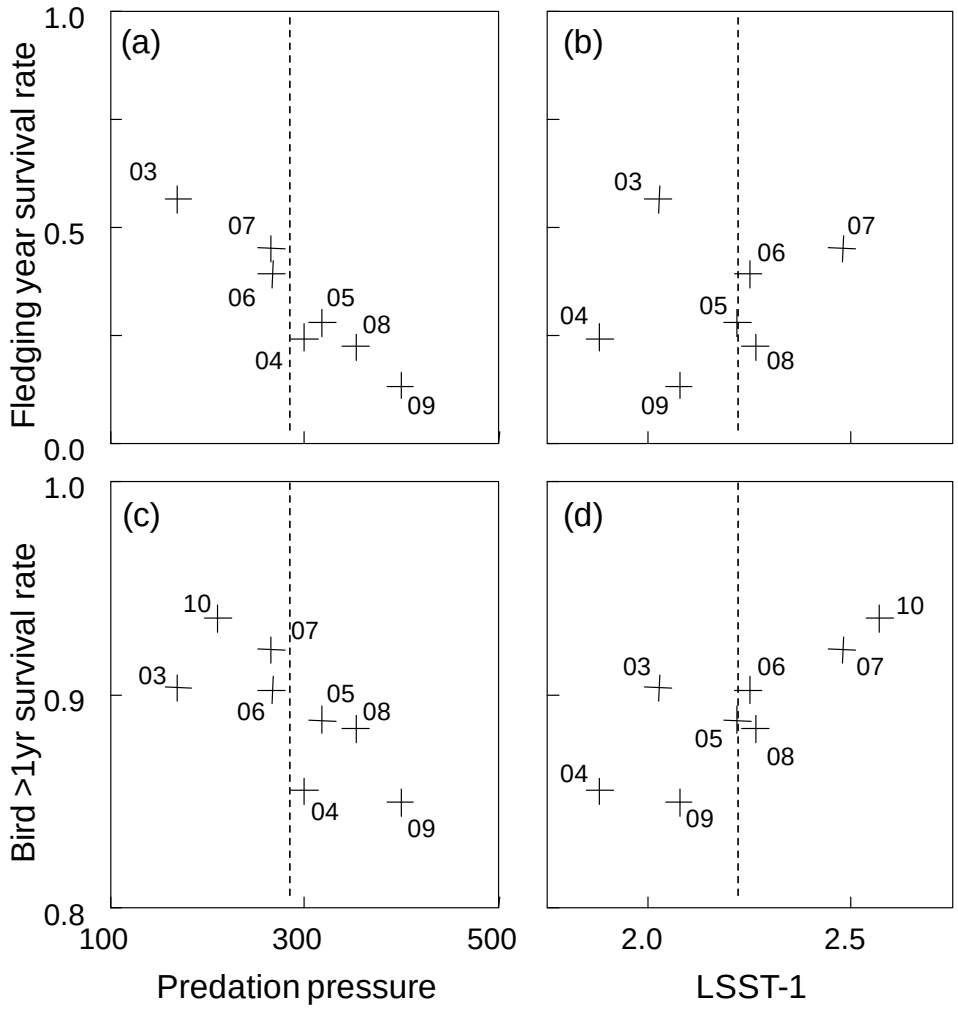


Figure 7. Survival of macaroni penguins in relation to different covariates by age class. Fledgling birds in relation to a) predation pressure (mean shown with dashed line); and b) $LSST_{-1}$ (mean shown with dashed line); Survival of macaroni penguins older than 1 yr. in relation to c) predation pressure; and d) $LSST_{-1}$.

Chapter 4

Sex-specific survival rates of adult macaroni penguins

Abstract

Demographic parameters vary among individuals of the same species, and can have a dramatic influence on population growth rate. The survival rates of adult macaroni penguins (*Eudyptes chrysolophus*) breeding at Bird Island, South Georgia, were investigated in relation to sex for a 10 year period (2003-2012). The estimation of demographic parameters was based on capture-recapture data modelled to examine temporal process variation between the sexes. Males and females did not differ in their survival or recapture probabilities, presumably because parental investment is shared equally between the sexes, and sexual dimorphism is small in this species.

Introduction

Individuals of different sexes may behave and therefore respond differently to environmental and demographic pressures (Coulson *et al.* 2001). Furthermore, size is likely to determine an individual's competitive ability, foraging efficiency and, ultimately, the costs associated with reproduction. For penguin species with low levels of sexual dimorphism, survival rates do not generally differ between the sexes. However, sex-specific breeding behaviour may increase the susceptibility of one sex to adverse extrinsic conditions. For example, female king penguins recruit to the breeding population at a younger age than males (Olsson and van der Jeugd 2002). Consequently, females are on average younger and less experienced than males and experience lower survival rates when prey availability is reduced. In Adélie penguins (*Pygoscelis adeliae*) the negative effects of flipper bands are more pronounced on females (Dugger *et al.* 2006), and finally, the extended (60 day) fast undertaken by male emperor penguins makes them more susceptible than females to adverse environmental conditions (Barbraud and Weimerskirch 2001; Jenouvrier *et al.* 2005).

Macaroni Penguins (*Eudyptes chrysolophus*) show limited sexual dimorphism in size, with the distributions of most phenotypic traits overlapping between the sexes (Williams 1995). Consequently the daily energy expenditure of both sexes is largely comparable when foraging outside of the breeding season (Green *et al.* 2009). Furthermore, previous studies have not shown dietary differences between the sexes (Bearhop *et al.* 2006; Cherel *et al.* 2007; Chapter 6). However, male and female macaroni penguins differ in one or more aspects of their breeding behaviour. Notably, males return to the breeding colony earlier in order to defend the nesting territory, and during the brood-guard phase, males fast and brood the chick continuously. In contrast, females produce the clutch of eggs and during chick-rearing fulfil the majority of the provisioning requirements (see Table 8, Chapter 6, for chronology of breeding phases). Consequently, levels of daily energy expenditure differ between the sexes at certain points in the breeding season (Green *et al.* 2009). These differences could result in fitness consequences that increase the susceptibility of one sex to environmental change. To investigate the influence of sex on survival and recapture probabilities, this study used mark-recapture modelling. The sex of macaroni penguins cannot be determined for birds that are <1 year old using bill dimensions (Williams and Croxall 1991). To avoid bias resulting from retrospective classification (Buckland, 1982; Nichols *et al.* 1994) this study was carried out separately from Chapter 3 and birds PIT tagged as chicks were not considered.

Methods

This analysis employed part of the data set analysed in Chapter 3. The materials and methods detailed in Chapter 3 are therefore also relevant here. All birds that were older than one at PIT tagging were sexed using bill dimensions at PIT tagging (Williams and Croxall 1991). The inaccurate sexing of a bird may occur at the extreme values of each sex, i.e. a small male or a large female (~88% success rate of correctly identifying sexes in macaroni penguins, Hart *et al.* 2009). Because these phenotypic differences may cause individuals to have slightly different survival rates compared to the rest of their sex, it was assumed that any bias due to the misidentification of individuals was negligible.

Data analysis

Capture-Mark-Recapture modelling of survival

Capture-mark-recapture models were fitted using Program MARK (Lebreton and Pradel, 2002). Conventional mark-recapture models assume that survival and recapture do not vary between individuals in a group, that no marks are lost and that the population is a closed

system (Lebreton *et al.* 1992). The starting model (here on referred to as the "global model") was constructed to have the highest number of parameters that was still biologically meaningful. All model structures are shown in Table 5. The goodness-of-fit of this model was assessed using the overdispersion parameter, median $\hat{c}$ (Cooch and White, 2011). Median $\hat{c}$ was estimated with a lower bound of 1.0, an upper bound of 4.0 and 100 replicates, and a score greater than 3 was taken to represent lack of fit (Lebreton *et al.* 1992). The error of all candidate models was increased by this value during model selection. All candidate models were nested within this model, and the most parsimonious was selected using the second-order Akaike Information Criterion (AIC_c) (Burnham and Anderson 2002). A difference of less than 2 AIC_c units was taken to suggest that competing models received a similar amount of support from the data. In this case the model with greater deviance explained was selected. A difference of more than 2 indicated strong support for the model with the lower AIC_c (Burnham and Anderson 2002).

Survival Probability (ϕ)

Survival was modelled as a function of sex and time. The effect of sex was tested as additive and interactive with time. The working hypothesis here was that sex-specific survival rates are more likely to occur during certain years (i.e. during certain extrinsic conditions).

Recapture Probability (p)

Recapture probability was allowed to vary from year-to-year and was tested as additive and interactive with time (Table 5). Similar to Chapter 3, model simplification involved fitting a reduced time-dependent variable with seasons grouped manually based on the duration the gateway PIT reader was in operation (p_{T3}): (1) not working (0 d: 2007); (2) working intermittently (1 - 100 d: 2009); and (3) working well (> 100 d: all other years). A constant recapture probability through time was also tested. Incomplete attendance histories at the individual level, caused by variable operation of the gateway PIT reader within seasons, precluded the separation of successful and failed breeding attempts, from birds returning to hold territory or moult (see Le Bohec *et al.* 2007). The incidence of missed breeding could therefore not be modelled (see Williams and Rodwell 1992; Crawford *et al.* 2006)

Results

For the global model with time dependent survival median $\hat{c}$ was estimated at 1.38 (SE = 0.02) (Table 5: model 5). Based on $\Delta QAIC_c$ and the Qdeviance explained, survival rates were best described in relation to time without an additive or interactive effect with sex (Table 5: model 2). In agreement with the results of Chapter 3, year-to-year variation in recapture rates was best described by the annual variation in the number of days that the gateway PIT reader was operational (Table 5: model 2). Recapture did not change in relation to sex ($\Delta QAIC_c < 2$; Table 5: model 2 vs. 1 and 3).

Discussion

Based on the available data, it appears that the survival rates of macaroni penguins are not sex-specific. This finding is in agreement with studies on other monomorphic penguin species (southern rockhopper penguins *Eudyptes chrysocome*; Dehnhard *et al.* 2013). In contrast studies on larger penguin species with low levels of sexual dimorphism have demonstrated the relationship between sex and survival rates to change between years in relation to environmental conditions. Here the favoured sex is dependent on the breeding ecology of the species (Barbraud and Weimerskirch 2001; Olsson and van der Jeugd 2002; Jenouvrier *et al.* 2005; Dugger *et al.* 2006).

The breeding behaviour of macaroni penguins differs between the sexes. Consequently, the impact of an unfavourable extrinsic event to each sex may depend on when the event occurs during the year. Further work may consider whether year-to-year variation in adult survival rates is dependent on the timing of climatic effects. The influence of sex on immature survival rates was not examined as part of this analysis. Male and female macaroni penguins are a similar size at fledging; therefore sex-specific differences in first year survival appear unlikely unless dispersal is segregated between the sexes.

Recapture rates were best modelled as a function of the gateway operation. The ability to detect an individual did not differ between the sexes or years. This study indicates that the fitness consequences of different breeding behaviour are equal in the macaroni penguin. This is in agreement with life history theory that males and females may work at different rates but incur similar reproductive costs (Stearns 1992).

Table 5. Modelling sex-specific survival probabilities of macaroni penguins breeding on Bird Island, South Georgia, that are older than age 1 (2003-2012).

No.	Model	$QAIC_c$	$\Delta QAIC_c$	k	QModel deviance
1	$\phi_t \ p_{s+T3}$	1487.51	0.00	14	123.71
2	$\phi_t \ p_{T3}$	1487.80	0.29	13	126.02
3	$\phi_t \ p_{s*T3}$	1488.14	0.63	17	124.34
4	$\phi_{s+t} \ p_{T3}$	1488.29	0.78	14	124.49
5	$\phi_{s*t} \ p_{s*t}$	1493.40	5.89	36	105.22
6	$\phi_{s*t} \ p_{s*T3}$	1494.26	6.74	7	114.23
7	$\phi_{s*t} \ p_t$	1497.27	7.10	27	113.17
8	$\phi_{s*t} \ p_{s+t}$	1497.60	9.76	28	111.46
9	$\phi_. \ p_{T3}$	1515.14	27.63	5	167.46
10	$\phi_s \ p_{T3}$	1516.35	28.84	6	166.66
11	$\phi_{s*t} \ p_s$	2183.21	695.70	20	807.25

Notes; Model fit is assessed using the lowest $QAIC_c$ with the difference between the best candidate model and other models specified ($\Delta QAIC_c$). Here, k is the number of parameters in the statistical model. Explanation of model notation (Cooch & White 2011): (ϕ) refers to the structure used to model survival probabilities, and (p) refers to capture probabilities. (s) indicates a sex-specific structure and (t) indicates a fully time-dependent structure; ($s*t$ or $s + t$) a fully time-dependent structure that is interactive or additive with sex; (.) a constant structure; and ($T3$) a fixed probability determined by the gateway operation.

Chapter 5

Unravelling the relative roles of top-down and bottom-up forces in driving population change

The data in this chapter is planned for submission to Ecology Letters as Horswill, C., N. Ratcliffe, J. A. Green, R. A. Phillips, P.N. Trathan, and J. Matthiopoulos. Unravelling the relative roles of top-down and bottom-up forces in driving population change in an oceanic predator.

Abstract

It is widely recognised that both top-down and bottom-up processes are important drivers of population change. Despite this, fluctuations in the demographic rates of pelagic species are thought to result largely from bottom-up processes. Macaroni penguins (*Eudyptes chrysolophus*) at South Georgia declined at *c.* 6% per year between 1985 and 2000, stabilising thereafter. Using a state-space demographic model we separate the processes underlying this trajectory, and quantified the relative importance of each driver in a sensitivity analysis. A comparison of demographic rates provided clear evidence that the population decline was attributable to an imbalance between recruitment to the breeding population and adult mortality. Stabilisation of the population trajectory reflected the release of productivity from density-dependence constraints, as well as improved survival rates.

Introduction

The predator-driven or "top-down" view of ecosystem control is widely accepted when considering terrestrial (Hairston *et al.* 1960), fresh water (Carpenter *et al.* 1985) and

intertidal ecosystems (Paine 1980). However, most population change in the open ocean, apart from those resulting from human exploitation, is largely thought to result from nutrient-driven or "bottom-up" control (Aebischer *et al.* 1990; Stenseth *et al.* 2002). Physical processes and nutrient fluxes dominate the structure and functioning of the open ocean (Behrenfeld *et al.* 2006). The prevailing view is therefore that top-down regulation in this system is unlikely (Pace *et al.* 1999). Despite this, the consequence of removing oceanic apex predators remains uncertain, and a number of studies have linked a change in the population size of oceanic predators to a marked change in community structure at lower trophic levels, indicative of top-down control (e.g. Estes and Duggins 1995; Bascompte *et al.* 2005; Frank *et al.* 2005; Springer and van Vliet 2014).

The polar ecosystem is receiving growing attention due to human-mediated changes driving biological change at both ends of the food chain; rapid regional warming (Vaughan *et al.* 2003) at the bottom and over exploitation of apex predator populations at the top (Agnew 2004). Unravelling the effects of bottom-up and top-down forcing on these open ocean ecosystems has thus been highlighted as an urgent task for polar scientists (Smetacek and Nicol 2005). The early view was that Antarctic and Sub-Antarctic oceanic systems were relatively simple; characterised by a large prey resource supporting an assemblage of apex predators (Laws 1977). However, an increasing number of studies have shown that the demography of particular "apex" predators is driven from trophic levels both above and below them (Schwarz *et al.* 2013; Horswill *et al.* 2014). By considering these predators as occupants of intermediate trophic levels, we establish a more robust framework in which to evaluate the opposing drivers of their population dynamics. The influence of different drivers on population dynamics is best assessed using integrated population models. In particular, Bayesian state-space approaches permit relationships between covariates and demographic processes to be informed using prior distributions to reflect available knowledge on the system (Buckland *et al.* 2004). Furthermore, missing data records can be imputed and the measurement errors inherent to ecological data can be explicitly accounted for in estimation and prediction uncertainty (Buckland *et al.* 2004).

Many populations of Antarctic and Sub-Antarctic marine predators experienced rapid population growth during the mid-1900s (Croxall and Prince 1979; Boyd 1993; González-Solís *et al.* 2000). This was largely linked to a "krill surplus" resulting from the extensive whaling era of the 1900s (Laws 1977). However, over the last few decades many of these

populations have declined (Reid and Croxall 2001; Woehler *et al.* 2001). For example, the population trajectory of macaroni penguins (*Eudyptes chrysolophus*) breeding on Bird Island, South Georgia, declined at 6% annually between 1985 and *c.* 2000, stabilising thereafter (Figure 8). Several studies on this population have examined the influence of single regulatory mechanisms (Reid and Croxall 2001; Forcada and Trathan 2009), but an examination of their survival rates recently highlighted the importance of considering multiple causal effects when investigating their survival rates (Chapter 3, Horswill *et al.* 2014). Consequently, the macaroni penguin is an ideal species for studying the relative importance of opposing effects. Here we use an age-structured state-space model to examine the mechanisms driving the observed population decline. This study incorporates a 28-year data set of population counts and productivity measurements, and a 10-year data set of survival estimates. We examine the links between individual covariates, demographic rates and the overall population trajectory, and by subjecting this model to a sensitivity analysis demonstrate the potential importance of each covariate in creating the observed population decline.

Methods

Study system

This study uses data collected from macaroni penguins at the Fairy Point colony on Bird Island, South Georgia (54° 00' S, 38° 03'W) between 1985 and 2012 (see Table 6 for length of individual time series). The total breeding population was counted annually at the start of the incubation phase (29th November - 10th December) to estimate population size. Chicks were counted shortly before fledging (16th February). Productivity was defined as the proportion of breeding pairs that reared a chick to the fledgling count date. Ground counts were repeated three times, or to within 10% of each other (methods are further detailed in CCAMLR 2004). Estimates of survival rates were obtained from a mark-recapture study based on passive integrated transponder tags (Chapter 3; Horswill *et al.* 2014).

Candidate covariates were identified from published information (Chapter 3; Horswill *et al.* 2014). Because productivity has not been previously examined in this population, candidate covariates were selected from information across Spheniscidae (Table 6). Covariates were standardised to $\bar{x} = 0$ and $\sigma = 1$. The relationship between demographic rates and the annual condition of individuals was examined using the mean of female body mass at the start of the breeding season (here on referred to as pre-breeding condition) and

the mean of fledging mass. All birds were weighed to the nearest 0.05kg using a spring balance (Pesola, Baar). Female birds were weighed to correspond with synchronous arrival at the colony (n=54 ±5 year^{-1}; 8-9th November). Chicks were weighed just prior to fledging (n=103 ±6 year^{-1}; 16-19th February). The influence of top-down control from predation pressure was examined using the number of giant petrel chicks (*Macronectes halli* and *M. giganteus*) reared to fledging. This is assumed to reflect the number of individual giant petrels foraging under central place constraint when the penguin chicks fledge. Giant petrels nesting within three study areas on Bird Island were visited weekly during the breeding season to determine individual productivity.

The influence of bottom-up control was assessed as a function of competition and environment. The breeding season foraging grounds and diets of macaroni penguins and Antarctic fur seals strongly overlap (Reid *et al.* 1996). The number of Antarctic fur seal pups raised to weaning was therefore included as a proxy for inter-specific competition. Annual fur seal productivity was estimated from twice-daily monitoring at the Bird Island study beach between November and January. In addition, the modelled population size of macaroni penguins was included as a proxy for intra-specific competition. Environmental variables included one local and two ocean-scale measurements. Local sea surface temperature anomalies (LSST) in the region associated with foraging during the breeding season (35.5°W to 44.5°W; 52.5°S to 54.5°S) was used to reflect local conditions such as upwelling that are thought to influence prey biomass within the continental shelf zone (Trathan *et al.* 2003). LSST data were obtained from the National Oceanographic and Atmospheric Administration (NOAA) International Research Institute (http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/.SSTa/). Following Horswill *et al.* (2014; Chapter 3) LSST was included with a 1-year lag for modelling survival rates. The number of years to parameter ratio prevented the influence of different lags being tested in the productivity model; therefore, SSTa was included for the year of observation. The El Niño/Southern Oscillation (ENSO) phenomenon and the Southern Annular Mode (SAM) were used to reflect remote forcing on the environment at South Georgia caused by variations in the circumpolar winds over the Southern Ocean, upwelling and SST anomalies (Meredith *et al.* 2008) that are also likely to influence local prey availability (Murphy *et al.* 2007). The bivariate ENSO time series (BEST) index was obtained from the NOAA Climate Diagnostics Center (http://www.cdc.noaa.gov/people/cathy.smith/best/), and the SAM index was obtained from the NOAA Climate Prediction Center (http://www.cpc.ncep.noaa.gov/). ENSO and

SAM were included in line with plausible physical lags; El Niño events are associated with warmer temperatures in the Scotia Sea region after approximately 2-years, whilst SAM is almost instantaneous (Meredith *et al.* 2008).

State-space population model

Parameters and hidden states estimated from the state-space population model included; 1. coefficients describing the relationship between different covariates and demographic processes; 2. missing (and thus imputed) segments of demographic and covariate time series; and 3. the magnitude and direction of different observation biases and imprecision. Inference was undertaken in OpenBUGS (http://www.mrc-bsu.cam.ac.uk/bugs/). Models were fitted by running three Monte Carlo Markov Chains (MCMC) for 10^5 iterations. The first 5000 draws were removed as burn-in. Each chain was initialised at different points in parameter space. Mixing and convergence of the MCMC chains was examined by visual inspection for all parameters and states estimated by the model. Convergence of the three chains was confirmed for all states and parameters using the Brooks-Gelman-Rubin diagnostic tool in the OpenBUGS software (all values <1.02).

Preliminary model selection

Incomplete time series of specific covariates prevented model selection from being implemented within the state-space framework. Preliminary selection of candidate covariates was therefore carried out using GLM analyses (Appendix S6). Re-estimation of the associated coefficients within the integrated analysis allowed the final parameters to be informed by the full demographic data set (Appendix S7).

Demographic model

Studies on banded penguins have indicated that recruitment can occur within the same year as first return following deferred reproduction (+1 yr.; Guinard *et al.* 1998). We took the mean age of recruitment to coincide with the maximum age of first return for this population; age 4 (Chapter 3; Horswill *et al.* 2014). In the absence of evidence for a significant gender difference in survival rates (Chapter 4) a 1:1 sex ratio was assumed and female numbers were modelled only; i.e. the number of breeding female birds (i.e. the number of breeding pairs), and the number of female chicks produced (i.e. half the total productivity). The deterministic transition matrix was based on 5 state variables; one fledgling, three sub-adult and one adult stage (Chapter 3; Horswill *et al.* 2014):

$$R_t = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & b_t \\ \phi_{f,t} & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_{a,t} & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_{a,t} & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_{a,t} & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_{a,t} & \phi_{a,t} \end{pmatrix} \quad (1)$$

Survival and productivity were modelled as binomial processes (following Matthiopoulos *et al.* 2013). Macaroni penguins lay two eggs, but very high mortality of the first-laid egg, means that they can effectively be viewed as laying a one-egg clutch (Williams 1995). Covariates were incorporated into the demographic rates by modelling the probability of survival or productivity as a logit-polynomial function.

The functions for adult and fledgling survival rates (eqn. 2-3) followed the model structure detailed in Horswill *et al.* (2014; Chapter 3). Inter-annual variability was induced though a combination of individual quality (fledging mass *M*), age-specific top-down control linked to predation pressure from giant petrels (*P*) and bottom-up control from environmental variables (LSST with a year lag, S_{t-1}) (Table 6):

$$\text{logit}(\phi_{f,t}) = \sigma_{f,t} + \sigma_t t \ + \sigma_2 M_t + (\sigma_3 + \sigma_4)\text{P}_t + \sigma_5 S_{t-1} \quad (2)$$

$$\text{logit}(\phi_{a,t}) = \sigma_{a,t} + \sigma_t t + \sigma_3 P_t + \sigma_5 S_{t-1} \quad (3)$$

Here, *f* and *a* denote birds in the fledging year or birds that are older than age 1, respectively. Age dependence was determined by using different parameters for the baseline survival of fledglings ($\sigma_{f,1}$) and adults ($\sigma_{a,1}$). The duplicated parameter ($\sigma_t t$) links the two age classes via an additive term (Chapter 3; Horswill *et al.* 2014). The fledgling function contained an extra coefficient on the predation effect (σ_4) to allow for an additional component of predation on juveniles (Chapter 3; Horswill *et al.* 2014).

The productivity model (eqn. 4) included the covariates selected through GLM model selection; female pre-breeding body condition (*A*), environmental forces (local sea surface temperature S_t, and El Niño with a 2-year lag E_{t-2}), intra-specific competition (*C*) and predation pressure (*P*) (Table 6). Environmental variables were incorporated with interaction terms on penguin population size to examine whether their influence changed

over the study period (Table 6). The working hypothesis was that environmental variability affects productivity more during periods with higher population densities leading to elevated levels of intra-specific competition:

$$\text{logit}(b_t) = \beta_t + \beta_1 A_t + \beta_2 E_{t-2} + \beta_3 C_t + \beta_4 P_t + \beta_5 S_t + \beta_6 (C_t E_{t-2}) + \beta_7 (C_t \, \text{S}_t) \quad (4)$$

The number of breeding females estimated by the process model was fed back into the productivity function as the auto-covariate *C*.

Observation model

The observation model allowed the posterior variance of the annual estimates of survival and productivity to be informed by the measurement errors associated with the observed data. Survival rates were informed by the confidence interval of the CMR estimates for survival rates. Productivity rates were informed by the estimated error associated with the counts at the colony (see Appendix S6).

Prior distributions

Due to model complexity, prior distributions for the covariate coefficients were specified as rescaled beta distributions (following Matthiopoulos *et al.* 2013). All prior distributions are detailed further in Appendix S6 and S7.

Missing data

Missing data points were specified as normal variates with precision calculated from the variance of the available data. To account for serial autocorrelation, predation pressure was modelled as a random walk through time. These structures are further detailed in Appendix S6.

Initialising the population structure

The number of breeding females in the starting year was estimated from the mean ground count for 1985 under a uniform prior. The total number of females in the population (i.e. across all of the 4 age-states) was modelled from this point estimate assuming a stable age structure with mean demographic rates calculated from the observed data (Leslie 1945). This assumes that the population was growing or declining at a constant rate prior to the study period considered here. Reports suggest a steady rate of increase between 1977 and 1985 (Woehler *et al.* 2001).

Model sensitivity

To quantify the relative importance of each covariate in determining the observed population dynamics, the model was rerun with that effect removed. The number of breeding pairs estimated by the full and covariate-reduced models (denoted N_t and n_t, respectively), were compared by calculating the mean squared residuals over the length of the time series (T):

$$\sigma^2 = \frac{1}{T}\sum_{t=1}^{T}\left(N_t - n_t\right)^2 \qquad (5)$$

The covariate reduced models were then ranked by this statistic to determine the most influential covariates.

Model validation

The final model was validated by examining whether the observed population time series could be recreated from the functional structure, the parameter estimates and the covariate data, with the demographic data removed. The initial population structure was stochastically assigned (Appendix S6), and the parameters were normal variates with an expectation and variance equal to the respective posterior distributions derived by the full model (Appendix S7). We considered sensitivity to the boundness of the prior used to impute the missing values of predation pressure by decreasing the variance on the random walk model (real sequential difference $\bar{x} = 72$; reduced sequential difference $\bar{x} = 35$). Although this restricts the predicted values of predation pressure into a smaller range than observed, it was used to highlight years when the model is particularly reliant on the imputed values of predation in order to explain the observed change in population size.

Results

Model fit

The modelled survival and productivity estimates were within the confidence intervals and count errors of the observed data (Figure 9B-D). Overall, the observed population trajectory for the number of breeding pairs was recreated convincingly by the full model (Figure 9A). Likewise, the median population trajectory was recreated when modelled as a function of the parameter estimates and the covariate data, without the demographic data (Appendix S8). There was a clear difference between the observed number of breeding pairs and the modelled value in 2006 (Figure 9A; Appendix S8). By reducing the variance

on the prior distribution used to impute the missing values of predation pressure, the ability to simulate population size declined slightly during 1988, 1991 and 1995 (Appendix S9).

Factors affecting survival rates

The additive term between the age classes indicated that survival rates increased during the study period (Appendix S7). In the older age class survival was slightly lower and more variable prior to 2000 than during the subsequent period of population stability (Figure 9B; Appendix S10). In contrast, survival rates in the fledgling age class showed large variability throughout the study period (Figure 9C; Appendix S10). Mean survival rates were $\bar{x} = 0.41 (\sigma = 0.19)$ during the fledgling year and $\bar{x} = 0.88 (\sigma = 0.05)$ from age 1 onwards. Survival rates peaked during 1988, 2001, 2003 and 2010, and were low during 1986, 1987, 1994 and 2009. The survival rates of both age classes were positively influenced by $LSST_{-1}$ and negatively influenced by predation pressure. The survival rates of fledglings were also positively influenced by fledging mass (Table 7; Appendix S7).

Factors affecting productivity rates

Productivity increased during the study period (lm: *df*=25, *F*=6.71, *p*=0.02; Figure 9D; Appendix S10). Based on the credible intervals of the parameter estimates, inter-annual fluctuations in productivity were driven by a negative association with population size and ENSO, and a positive association with pre-breeding condition and predation pressure (Appendix S7). The direction of the relationship with LSST or interactions between environmental effects and population size could not be resolved based on the posterior credible interval (Table 7; Appendix S7). SAM_0 and the proxy for inter-specific competition were removed during the preliminary model selection (Table 6). However, the significance attributed to intra-specific competition as well as the dietary overlap with Antarctic fur seals during the breeding season (Reid *et al.* 1996) may suggest that the removal of inter-specific competition was due to cross-correlation of this variable with intra-specific competition (Reid and Croxall 2001).

Factors affecting the population trajectory

Prior to 2000, the rate of recruitment for macaroni penguins at Bird Island was 0.10 and the rate of adult mortality was 0.14 (Appendix S10). After 2000, the rate of recruitment was 0.12 and the rate of adult mortality was 0.10 (Appendix S10). The population trajectory was most sensitive to the influence of predation pressure on survival rates. Here, the relationship with birds older than age 1 was considerably more influential (Table 7). Of the

other covariates, the effects of $LSST_{-1}$ on adult survival and of predation on productivity were the largest (Table 7). However, the parameter estimates for the standardised covariates (pre-breeding condition, ENSO, predation) indicate that the effect of predation on productivity was marginal in comparison to these other two standardised drivers (Appendix S7). We therefore infer that the influence of this relationship in determining the observed population dynamics was because the missing values of predation pressure were partly informed by the productivity process during the integrated analysis. Removing predation from the productivity model thus reduced the ability to determine the effect of predation pressure on survival.

Missing covariate data

The missing predation pressure time series segment was slightly more variable (de-standardised $\bar{x}_{<2000} = 226.53, \sigma_{<2000} = 75.84$) than the period of observed data (de-standardised $\bar{x}_{\geq 2000} = 267.92, \sigma_{\geq 2000} = 67.55$; Figure 10A). Missing data for the fledging mass of macaroni penguin chicks and pre-breeding condition of adults were similar to the observed values (Figure 10B-C).

Discussion

We sought to evaluate the population trajectory of an oceanic predator as a function of the bottom-up and top-down covariates that influence demographic rates. The rate of decline for this population of macaroni penguins between 1985 and 2012 was broadly similar to the overall rate reported for Bird Island, as well as other large colonies on western South Georgia (Trathan *et al.* 2012). It therefore seems possible that the mechanisms highlighted here may have influenced populations across this region.

Factors influencing survival rates

Williams and Rodwell (1992) reported the survival rates of adult macaroni penguins from Bird Island to be $\bar{x} = \sim 0.75 (\sigma = \sim 0.06)$ between 1987 and 1990. The rates estimated in the present study for the same period are higher, but this is likely to reflect incomplete recapture in the Williams and Rodwell (1992) study. Furthermore, impaired survival due to flipper-banding (Saraux et al. 2011a) may have reduced the survival rates estimated in that earlier study. In agreement with Horswill *et al.* (2014; Chapter 3), the present study estimated survival rates during the fledgling year to be generally lower than the older age class; however under certain conditions (i.e. a low predation pressure and an elevated fledging mass) the two age classes experienced comparable survival rates. The mortality

rates of fledgling macaroni penguins were on average double that of increasing populations of southern rockhopper penguins (*Eudyptes chrysocome*) in the Falklands also resighted using implanted PIT tags (Baylis *et al.*, 2013). After accounting for phylogeny, the survival rates of birds typically increase in relation to body size (Lindstedt and Calder, 1976). Given that rockhopper penguins are smaller than macaroni penguins but the observed difference in survival is in the opposite direction, it is likely that the difference reflects extrinsic conditions.

Low survival rates were consistently associated with elevated levels of predation pressure. Studies from Bird Island report the diet of giant petrels to be dominated by adult macaroni penguins during the breeding season (Hunter 1983). As well as direct predation of macaroni penguins by giant petrels, this may also reflect scavenging on macaroni penguins killed by Antarctic fur seals (Bonner and Hunter 1982). Given the likely correlation between these effects, the predation pressure covariate may reflect predation by giant petrels and fur seals. Predation pressure is estimated using the productivity of giant petrels at Bird Island, however, little is known about what causes this to vary between years. It is notable that during years where macaroni penguins experienced low survival rates, other seabird and seal species that breed on Bird Island also reported poor survival and breeding performance. For example, during 1987, the survival rates of macaroni and gentoo penguins (*Pygoscelis papua*) were low (Williams and Rodwell 1992), and following the 1987 winter, delays in breeding were noted in Antarctic fur seals (Duck 1990) and gentoo penguins (Williams 1990). A delay in the onset of breeding could indicate unfavourable environmental conditions during the preceding winter (e.g. Barbraud and Weimerskirch 2006). During 1994, lower reproductive output was reported for macaroni penguins, Antarctic fur seals, gentoo penguins and black browed albatross (*Thalassarche melanophrys*; Reid and Croxall 2001), and during 2009 high adult mortality and a dramatically reduced rate of productivity were observed in gentoo penguins (BAS unpublished data). The concurrence of trends across multiple species may indicate that some form of combined resource (bottom-up) and predatory (top-down) control could be operating. Future studies should therefore consider the possible interactions between these effects.

The mean survival rates of both age classes increased over the study period. At South Georgia, SST slightly decreased during the 1980s and 1990s, equivalent to a cooling of 0.14 ^{0}C (Meredith *et al.* 2008). Furthermore, predation pressure did not appear to show an

obvious trend over the study period. Whilst we have seen that predation and SST can influence the survival rates of macaroni penguins, they were apparently not the main drivers of the overall increase in the survival rates reported here. In previous studies on this population, ENSO and SAM were not highlighted as influential drivers of survival rates (Horswill *et al.* 2014). However, since these are intermittent effects (i.e. El Niño occurs approximately every 4-years, SAM fluctuates on timescales of weeks to decades) the lack of influence assigned to these covariates in our earlier analysis (Chapter 3; Horswill *et al.* 2014) may have been due to the relatively small number of years considered (n=10). Alternatively, the dynamic propagation of ENSO and SAM throughout this ecosystem (Meredith *et al.* 2008) might make the use of a constant lag unsuitable. Methodological advances in carrying out formal model selection within state-space models and further long-term data collection may support the re-evaluation of these covariates.

Three anomalous mortality events potentially occurred between 1985 and 2000 each lasting 1-2 years. Low survival rates during the fledging year will not influence the size of the breeding population until that cohort recruits. Therefore, if the mortality event was immediately preceded by low survival (i.e. during 1986, 1987 and 1994), we infer that this was driven by the older age class only. Population growth rates of long-lived species are typically most sensitive to changes in adult survival rates (Lebreton and Clobert 1991). However, when the population declined in the absence of low adult survival rates (i.e. between 1989 and 1991), the driving mechanism was inferred to be low rates of productivity and fledgling survival occurring four years earlier in the time series. For example, below-average productivity and low fledgling survival produced two small cohorts during 1986 and 1987; the small 1986 cohort also experienced low adult survival rates during 1987. Subsequently, a comparatively low number of individuals recruited to the breeding population during 1990 and 1991, and the population declined. This effect also occurred following the mortality event in 1994, where low numbers were recruited during 1999. On this latter occasion, high adult survival rates during 1998 and higher levels of productivity associated with a lower population density buffered the expected impact.

The mortality events (1986, 1987 and 1994) were associated with elevated levels of predation pressure. The sensitivity analysis on the priors used to model the missing values of predation pressure indicated that predation pressure was a key driver during these years. However, during 2006 the modelled and the observed number of breeding pairs differed

suggesting that in certain years the observed number of breeding pairs could not be determined from the demographic functions alone. Our models assumed no missed breeding because incomplete attendance histories at the individual level, caused by variable operation of the gateway PIT reader within seasons precluded its identification. However, macaroni penguins may skip individual breeding attempts following adverse winter conditions (Williams and Rodwell 1992). By assuming that all adults are accounted for by the observed population size, the imputed values of survival during 1986, 1987 and 1994 may be slightly underestimated and the corresponding values of predation pressure overestimated, albeit not beyond a realistic range. Further work should consider the effect of breeding proportions on population size in order to quantify this intermittent effect.

Factors influencing productivity

Year-to-year variation in productivity was driven by changes in ENSO, pre-breeding condition, predation pressure and population size. The mean productivity rate was similar to other decreasing populations of macaroni penguins that breed in colonies of comparable size ($\bar{x} = 0.46 - 0.57$ chicks pair^{-1}; Crawford et al. 2006). However, productivity increased over the study period and by 2011 productivity rates were comparable to those observed for increasing populations of southern rockhopper penguins ($\bar{x} = 0.64$ chicks pair^{-1}; Baylis *et al.* 2013). Between 1976 and 2003 the amount of krill in the southwest Atlantic is thought to have declined by 80% (Atkinson *et al.* 2004). Whilst some researchers have proposed that density-independent factors, such as sea-ice extent or the frequency of extreme El Niño events have driven these changes (Atkinson *et al.* 2004; Murphy *et al.* 2007), others have proposed a more local effect resulting from the elevated numbers of predators in the system (Trathan *et al.* 2012). Productivity of macaroni penguins increased over the study period, but fledging mass and pre-breeding condition did not change. We therefore infer that krill availability per capita was greater at lower population densities; i.e. krill biomass has declined at a slower rate than the population of macaroni penguins since 1985 (i.e. <70%).

ENSO is thought to change the environmental carrying capacity of this ecosystem (Murphy *et al.* 2007). In agreement with other penguin-demography studies productivity decreased during El Niño events, possibly indicating reduced food availability during these years (e.g. Chambers 2004). The effect of ENSO did not appear to change in relation to population size indicating that El Niño events created elevated levels of intra-specific competition even at lower population densities. This may indicate that the carrying

capacity of the breeding season environment has declined over the study period or alternatively that the influence of ENSO has changed. Since the late 1970s the conventional canonical El Niño has become less frequent and a different kind of El Niño has become more common (Ashok *et al.* 2007). As these events differ in both the location of maximum SST anomalies and tropical–mid-latitude teleconnections (Ashok *et al.* 2007), linkages to the Southern Ocean and Antarctica via atmospheric and oceanic processes are also likely to differ (Lachlan-Cope and Connolley 2006). However, ENSO had a marked preponderance of El Niño events compared with La Niña events between 1983 and 2008 (Meredith *et al.* 2008). Thus, whilst this study indicates that ENSO can influence productivity it is unlikely to have driven the increasing trend in productivity as the change in productivity based on changes in ENSO would be predicted in the opposite direction to that observed.

Previous studies indicate that macaroni penguins only return to breed above a certain condition threshold (Williams and Rodwell 1992; Crawford *et al.* 2006). In support of this concept, we found a negative association between pre-breeding condition and productivity. Pre-breeding condition may be driven by conditions at winter foraging grounds, however as penguins return to forage in waters close to the colony for at least a week prior to coming ashore to breed (Adélie penguins; Tierney *et al.* 2008) this relationship may also reflect conditions more local to colonies. A positive association between predation pressure and productivity is also indicated. Observational studies propose that giant petrels can predate on penguin chicks at the colony (Le Bohec *et al.* 2003), however it appears that this behaviour is not influential to macaroni penguins at Bird Island. This may reflect resource portioning by giant petrels at different points of the breeding season (i.e. fur seal carcasses, penguins, krill; González-Solís *et al.* 2000). The positive association between predation pressure and productivity is therefore likely to reflect an environmental effect that favours both species during the chick-rearing phases.

Pre-breeding condition and predation did not show an overall trend during the study period. It therefore appears that productivity increased as a function of reduced levels of intra-specific competition as the population decline. A negative relationship between population density and productivity has been documented in several seabird species (Weimerskirch and Jouventin, 1987; Frederiksen and Bregnballe, 2001), including penguins (southern rockhopper penguins; Baylis *et al.* 2013). Here, the proposed

mechanism is principally a product of intraspecific competition; where levels of prey availability increased as the population declined.

Population trajectory

Our model has teased out the processes underpinning the population trajectory within our study period. The population of macaroni penguins considered here declined rapidly between 1985 and 2000. During this period the rate that birds recruited to the breeding population was lower than adult mortality, and three large mortality events occurred (1986, 1987 and 1994) in association with elevated levels of predation pressure. A clear breakpoint in the population trajectory occurred *c.* 2000. Whilst this prominent feature was not traceable to a single demographic process, the recreation of this trend in a model where the majority of the observed demographic data was removed suggests that the principle mechanisms underpinning this trend have been captured. We infer that the demographic rates experienced between 1985 and 2000 caused the population to decline below the carrying capacity during the breeding season. The reduced levels of intra-specific competition as the population declined then allowed rates of productivity and survival to increase. Stabilisation of the population after 2000 was thus a product of survival rates becoming on average higher and less variable as well as a density-dependent increase in productivity.

Conclusion

Low rates of productivity and survival during the beginning of the study period caused population decline. The population trajectory was most sensitive to changes in predation pressure, however in the absence of a significant change in predation during the study period the observed population change could not be attributed to this driver. The stabilisation of the population trajectory was principally driven by an increase in survival and productivity rates, where productivity increased in response to reduced levels of bottom-up control as the population declined. The future stability of this population will thus depend on the carrying capacity of the environment supporting productivity rates at their present level, in addition to the population size and breeding success of giant petrels not increasing so that adult survival rates can remain stable. This study demonstrates the additional insights that can be collated by using models with increased precision.

Table 6. Candidate covariates for modelling each demographic process of macaroni penguins at Bird Island, South Georgia, with preliminary model selection criteria and the length of available time series.

Parameter	Covariate	Data availability	Model Selection	Reference of effect
Survival (Fledging year)	Fledging mass	1988-2012	CMR*	Horswill *et al.* 2014
	Predation	2001-2012	CMR *	Horswill *et al.* 2014
	$LSST_{-1}$	1985-2012	CMR *	Horswill *et al.* 2014
Survival (>1 year)	Predation	2001-2012	CMR *	Horswill *et al.* 2014
	$LSST_{-1}$	1985-2012	CMR *	Horswill *et al.* 2014
Productivity	Pre-breeding condition	1988-2012	GLM*	Crawford *et al.* 2006
	Predation	2001-2012	GLM*	Le Bohec *et al.* 2003
	Population size	1985-2012	GLM*	Ainley *et al.* 1983
	Fur seal competition	1985-2012	GLM	Trathan *et al.* 2012
	$LSST_0$	1985-2012	GLM*	Chambers *et al.* 2004
	$ENSO_{-2}$	1985-2012	GLM*	Chambers *et al.* 2004
	SAM_0	1985-2012	GLM	Forcada and Trathan 2009

Notes: Model selection undertaken in a capture-mark-recapture (CMR) framework (Chapter 3) or a GLM structure (see Appendix S6). Asterisk denotes covariates selected for inclusion in the state-space framework. See main text for covariate notation.

Table 7. The relative importance of each covariate in determining the population trajectory of macaroni penguins at Bird Island, South Georgia (most influential covariate shown in bold).

Demographic process	Covariate	Direction of trend	Sensitivity to popualtion trajectory
Survival (Fledging year)	Predation	-	88.09
	$LSST_{-1}$	+	1.06
	Fledging mass	+	1.42
Survival (>1 year)	Predation	-	**374.57**
	$LSST_{-1}$	+	6.03
Productivity	Predation	+	7.41
	Pre-breeding condition	+	5.06
	$ENSO_{-2}$	-	3.45
	Population size	-	3.09
	Population size * $ENSO_{-2}$	-/+	1.89
	Population size * $LSST_0$	-/+	0.29
	$LSST_0$	-/+	0.06

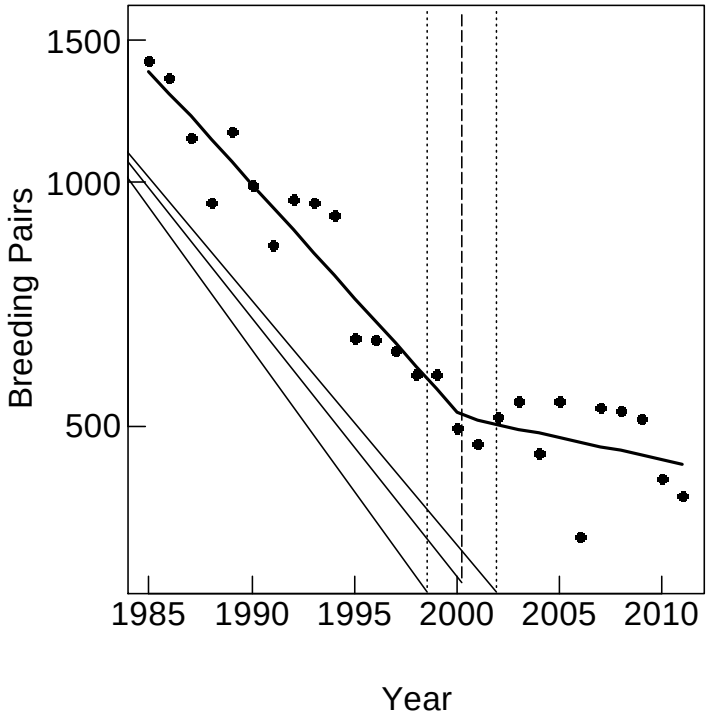


Figure 8. Population trajectory of macaroni penguins at Bird Island, South Georgia (1985-2011). Scaling on the y-axis is $\log_e$, values are back-transformed.. The breeding population declined at 6% (SE=0.01) per year until c. 2000, the trend thereafter could not be reliably resolved, a decline of 1% (SE=0.01) (broken-stick GLM shown in black line fitted in Program R with the "segmented" library, Muggeo 2008). The estimated breakpoint in the trend and standard error (1.6 years) are shown with vertical dashed and dotted lines, respectively.

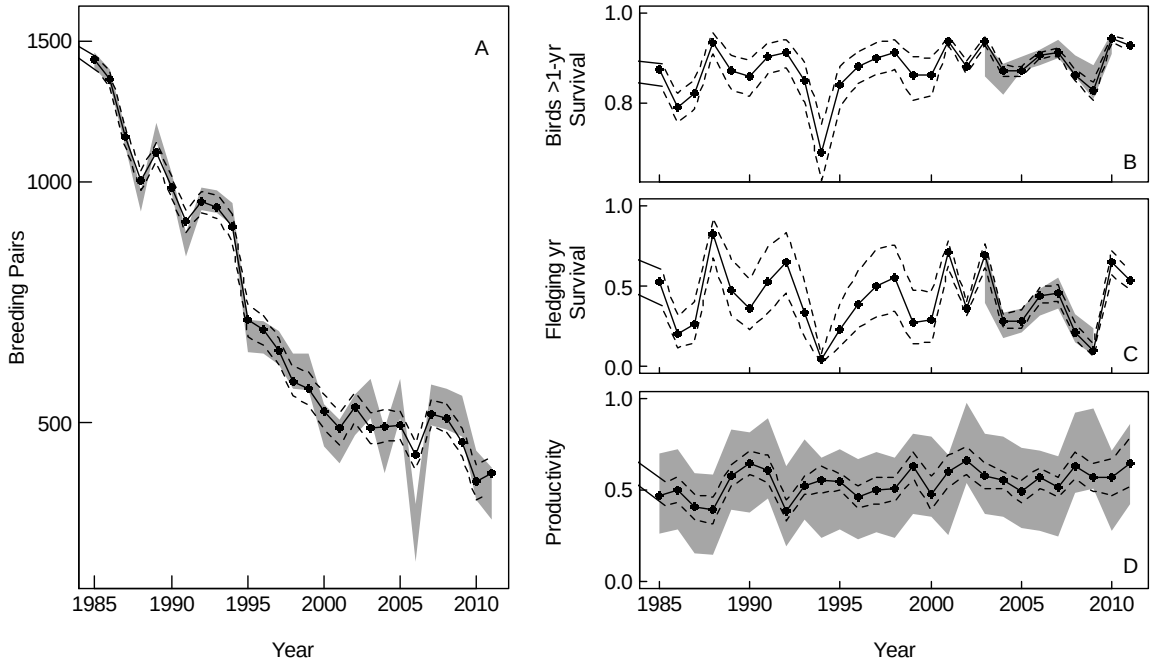


Figure 9. Demographic rates of macaroni penguins at the Fairy Point colony, Bird Island, South Georgia (1985-2011). A) Modelled population trajectory. Observed trajectory with confidence interval estimated from the repeated counts (shaded in grey), modelled trajectory with 95% credible interval (median values shown with markers and solid lines, 95% credible interval shown by dotted lines). Scaling on the y-axis is $\log_e$, values are back-transformed. B-C) Time series of posterior estimates of survival rates (median values shown with markers and solid lines, 95% credible interval shown by dotted lines). The 95% confidence intervals of the independent survival estimates (from capture-mark-recapture data), are shown as the grey shaded band; B) birds >1-year; C) fledglings; D) Posterior distribution of productivity estimates by year (scaled to reflect chicks $pair^{-1}$). Median values shown with markers and solid line, 95% credible interval shown with dotted line. Observed productivity estimates shaded in grey with confidence interval taken from the repeated counts.

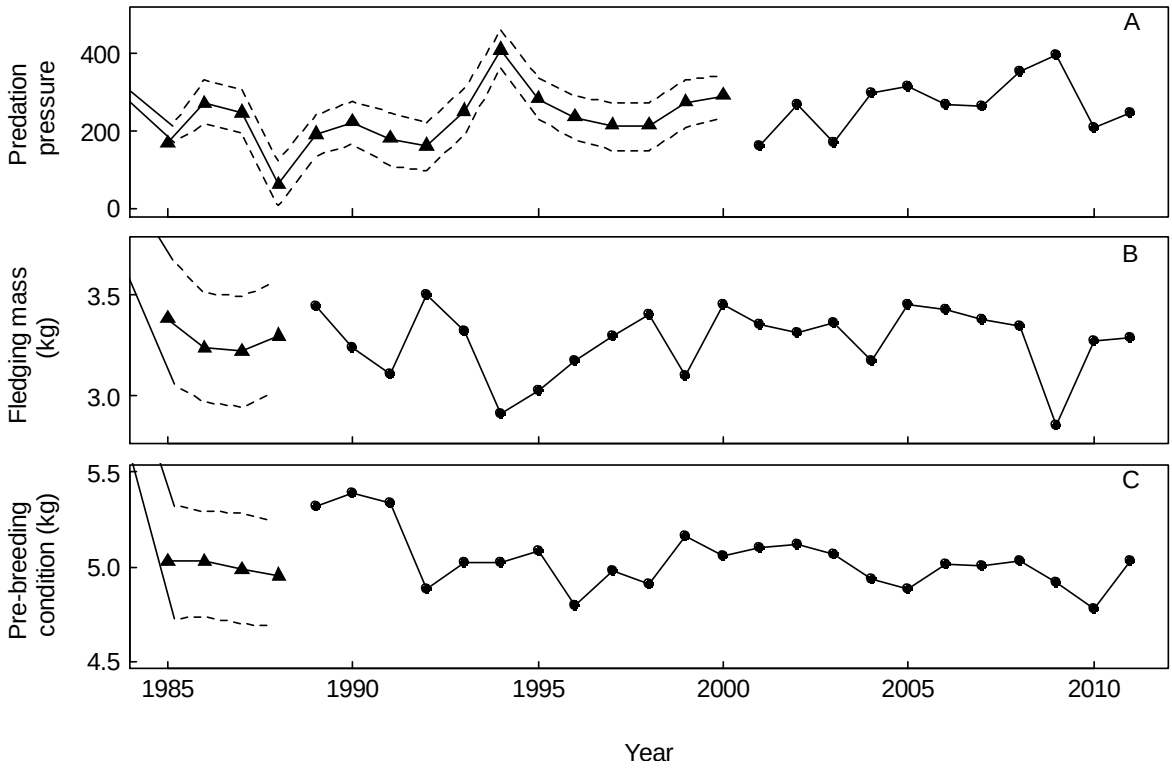


Figure 10. Time series of covariates used to model the population trajectory of macaroni penguins at Bird Island, South Georgia, with inference of missing data segments. A) Predation pressure from giant petrels over time; B) Fledging mass over time;. C) Pre-breeding condition of adults over time. Observed values (black circles) and predicted values (black triangles with 95% credible interval).

Chapter 6

Dietary specialisation reflects changing constraints on foraging in the macaroni penguin

The data in this chapter is in review at Oecologia as Horswill, C., J. Matthiopoulos, N. Ratcliffe, J. A., Green, P. N. Trathan, R. A. R. McGill, R. A. Phillips, and T. C. O'Connell. Dietary specialisation reflects seasonal variations in foraging range in the macaroni penguin.

Abstract

Although an increasing number of studies are finding evidence that generalist populations are actually made up of relatively specialised individuals, the ecological mechanisms that create and maintain individual specialisation remain poorly understood. We used stable isotope analysis to investigate dietary specialisation within a colonially breeding species, the macaroni penguin (*Eudyptes chrysolophus*), and examine temporal variation in specialisation as a function of sex, breeding parameters (timing of breeding and incubation trip duration) and foraging constraints (free-ranging and differing levels of central place constraint). Individual differences in diet were apparent across different sample types and supported by independent tracking data. During phases of the breeding season associated with a relaxed central place constraint, different individuals appeared to make distinct diet choices that remained highly consistent from year-to-year. In contrast, during phases of the breeding season with restricted central place constraint and reduced diversity in available resources, birds had a more homogenous isotope signature. This study indicates that colonially breeding, generalist species may employ individually specialised foraging strategies in response to seasonal variations in foraging range and prey availability at the foraging sites.

Introduction

Generalist predators will switch to alternative prey when preferred foods are not readily available (Schoener 1971; Roughgarden 1972; Krebs *et al.* 1977). Within natural generalist populations, diversity in resource use can appear as short-term differences among individuals, as well as longer-term specialisation within individuals (Bolnick *et al.* 2003; Araújo *et al.* 2011). Several studies have tested hypotheses as to how the strength of individual specialisation varies across ecological contexts (Araújo *et al.* 2011), and in particular its relationship with inter- and intra-specific competition (and associated phenotypic characters; e.g. Roughgarden 1972; Bolnick 2001; Kobler *et al.* 2009; Svanbäck *et al.* 2011). However, links between individual specialisation and the mechanisms that generate competition remain poorly understood (see also Layman *et al.* 2007; Herrera *et al.* 2008; Darimont *et al.* 2009).

Spatial and seasonal heterogeneity in resources, and individual reproductive constraints can change the diversity of prey available to a population, potentially altering the levels of intra- and inter-specific competition a population experiences (Araújo *et al.* 2011). For example, colonially breeding animals must return to a central location in order to provision offspring (Orians and Pearson 1979). During this period, conspecifics are concentrated within a restricted foraging range where the same prey field is effectively available to all individuals. For colonial species that do not hold feeding territories, such as pelagic seabirds and seals, individual differences in foraging behaviour during the breeding season can therefore be considered to occur because of individual foraging decisions. For most seabirds, foraging constraints change during the breeding season in relation to the varying demands associated with nest defence, incubation and chick rearing. Trips are usually shortest during the initial weeks post-hatching (the brood-guard period, Table 8) when the offspring require constant parental protection from predators, thermoregulatory support, and regular small meals. The length of foraging trips extends in later chick-rearing when the offspring can be left alone between meals (the post-guard or crèche period, Table 8), and are longest during the incubation and, in penguins, during the pre-moult periods when birds need to build up essential body reserves for the subsequent fast (Williams 1995). During these longer trips, central-place constraints may be partially relaxed but without the full freedom afforded to individuals during the non-breeding season when most seabird species are entirely pelagic (Hatch *et al.* 2000; Guilford *et al.* 2009; Ratcliffe *et al.* 2014).

Individual variation in foraging strategies has been suggested in a number of different seabird species, and in some cases this has been linked to sex- or age-related differences in size, experience or dominance (Weimerskirch *et al.* 2007; Phillips *et al.* 2011). Furthermore, a growing number of studies have used techniques such as stable isotope analysis to indicate that individuals consistently specialise in these strategies over time (Woo *et al.* 2008; Ceia *et al.* 2012). Stable isotope analysis provides an alternative to the traditional ways of determining diets from direct observation, analysis of faeces or stomach contents (DeNiro and Epstein 1978; 1981). Using this technique dietary variation can be resolved over different timescales by consideration of tissue-specific isotopic turnover rates; whereby, analysis of a particular tissue can provide an integrated dietary record for a specific period (Dalerum and Angerbjörn 2005). Stable isotope analysis has recently indicated that macaroni penguins (*Eudyptes chrysolophus*) may display individual dietary variation during particular phases of the breeding cycle (Bearhop *et al.* 2006; Cherel *et al.* 2007). Here, we combine isotopic analyses of several different sample types with tracking data in order to examine short–term dietary variation among individuals, and long-term individual specialisation in macaroni penguins. We set our findings in the context of changing foraging constraints imposed by the varying demands of the breeding cycle.

Methods

Stable isotope samples

To examine temporal variation in the diet of macaroni penguins, samples were collected in different years and within different stages of the breeding season from breeding birds at the Fairy Point colony on Bird Island, South Georgia (54° 00’ S, 38° 03’W). Each breeding season lasts from egg-laying in November to chick-fledging and adult moult in March/April (Table 8). Throughout the text a breeding season is referred to by the year in which the chick fledged. Multiple sample types were collected in order to examine stable isotope ratios across different temporal scales. Black (dorsal) feathers were collected from adults prior to moult in 2002, 2003, 2004 and 2012. To assess differences in stable isotope ratio associated with pigmentation, the individuals sampled during 2012 were also sampled for white (ventral) feathers prior to moult (n=20). To assess long term consistency in stable isotope ratio, the individuals sampled during 2012 were also sampled for black feathers after moult. Individuals were recognised by their passive integrated transponder (PIT) tags (Texas Instruments, USA) which were scanned using a hand-held reader (ISO RFID stick reader RS320-3-60, Allflex, Vitré). Birds were sexed using bill dimensions (Williams and Croxall 1991); sexes were also verified by monitoring nest attendance patterns. Macaroni

penguins renew their entire plumage each year during a single moulting period (Brown 1986). Feathers are metabolically inert and therefore represent diet at the time of synthesis. Given the turn-over rate of blood plasma and internal tissues from which nutrients for feather formation are derived, stable isotope ratios in feather tips correspond largely to diet during the 2-week pre-moult foraging trip, with potentially a small residual signal from the late crèche period (Cherel *et al.* 2005). Feathers sampled before moult therefore represent the pre-moult diet in the preceding breeding season, whereas feathers sampled after moult are representative of the season of sampling. Sampling of feathers from different birds within a year provides a measure of diet variation among individuals, and sampling of the same individual in different years provides a measure of within-individual specialisation.

Blood samples were collected from breeding birds during each phase of the 2012 season (see Table 8 for chronology of breeding phases; Appendix S11 for sample sizes). To minimise disturbance, individuals were selected from a sample of 200 nests that were marked throughout the colony at the start of the breeding season. Samples were taken from the brachial vein (non-heparinised syringe, and 23-gauge needle, Microlance; Samour *et al.* 1983). To avoid the use of anticoagulants (Lemons *et al.* 2011), samples were centrifuged within 5 minutes of collection using a small bench-top centrifuge (MSE Micro Centaur, Sanyo, London) powered by a portable inverter generator (1000w EU inverter 10i, Honda, Tokyo), and the plasma decanted. Fresh guano was collected opportunistically when handling birds for blood sampling. Guano was immediately sealed in a microcentrifuge tube (Eppendorf, Hamburg) to minimise nitrogen volatilization (Jianjun *et al.* 2009). All samples were frozen and stored at -20˚C until prepared for analysis (see Appendix S11 for sample sizes). The turnover rate of penguin blood cells was estimated at *c.* 32 days (Cherel *et al.* 2007; Thiebot *et al.* 2014) and for plasma samples *c.* 7 days (Barquete *et al.* 2013). Guano was taken to represent diet within *c.* 3 days (Bird *et al.* 2008). The isotope ratios of carbon and nitrogen within each tissue type depends on the isotopic fractionation processes (Peterson and Fry, 1987). The different turnover rates associated with the sample types considered here allowed information to be obtained at different temporal scales. Because direct comparisons between the absolute values of the different sample types are not made, a tissue correction factor was not employed (Dalerum and Angerbjörn 2005).

Breeding parameters

As part of the 2012 study, marked nests were visited daily to record the timing of laying (expressed as the number of days since 1 November; hereon referred to as timing of

breeding) (Table 9). During the incubation phase, each member of the breeding pair incubates the egg individually whilst the other partner undertakes a single extended foraging trip (Table 8). The attendance of the marked nests was checked daily to estimate the duration of each incubation trip to ±1 day.

Sample preparation for stable isotope analysis

Feather tips are synthesised at sea during the pre-moult trip, and might differ in $\delta^{13}C$ and $\delta^{15}N$ from the rest of the feather (Cherel *et al.* 2005). Therefore, only the top 5 mm of vane was retained for analysis. Two feather tips from each individual were used for the stable isotope analysis. Feathers were cleaned of surface contaminants using a 2:1 chloroform: methanol rinse, repeated twice for 30 minutes in an ultra-sonic bath, followed by the same treatment using 1:2 chloroform: methanol rinse, and a final water rinse (Folch *et al.* 1957). Feathers were then freeze-dried. To test for ^{15}N fractionation and ^{13}C enrichment associated with the cleaning process, cleaned and uncleaned black feathers collected from the same individual were prepared separately for stable isotope analysis (n=16, all males; Sweeting *et al.* 2006). It was assumed that the cleaning process would not differ due to feather pigmentation. In addition to test for pigment enrichment of ^{13}C and ^{15}N, black and white feathers collected from the same individual (n=20) were prepared following the same cleaning procedure (Michalik *et al.* 2010). Blood cells, blood plasma and guano samples were freeze dried for 12-24 hours. Dried red blood cells and guano were homogenised using a ball mill (TissueLyser II, Qiagen, Manchester). This was unnecessary for dried plasma due to the sample volume and consistency.

Carbon and nitrogen isotopic measurements were determined by continuous-flow isotope ratio mass spectrometry. Feathers, blood cells and plasma were analysed at the Scottish Universities' Environmental Research Centre (East Kilbride, UK), and guano samples were analysed at the Goodwin Laboratory, University of Cambridge (UK). All analyses were performed using an automated elemental analyzer (Costech ECS 4010, Milan, Italy) coupled in continuous-flow mode to an isotope-ratio-monitoring mass-spectrometer (Thermo Fisher Scientific Delta V mass spectrometer, Bremen, Germany). Single subsamples of 0.7mg aliquots were analysed in tin capsules. To correct for instrumental drift, each analytical sequence included 3 internal standards (Gelatine [Fluka, Germany]; Glycine and Alanine [Sigma–Aldrich, Germany]) for every 10 unknown samples of blood and feathers, and 3 internal standards (Caffeine [IAEA, Austria]; Alanine and Nylon [Sigma–Aldrich, Germany]) for every 16 unknown samples of guano. Stable isotope

concentrations are measured as the ratio of the heavier isotope to the lighter isotope relative to the international standards VPDB (carbon) and AIR (nitrogen) (Hoefs 1997). Isotopic results are reported as δ values ($\delta^{13}C$ and $\delta^{15}N$) in parts per 1000 or 'per mil' (‰) values, using the calculation:

$$\delta X = [(R_{sample} / R_{standard})-1] \times 1000$$

where *X* is ^{15}N or ^{13}C, and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Based on replicate measurement of laboratory and international standards, measurement precision of both $\delta^{13}C$ and $\delta^{15}N$ was estimated to be ≤0.2‰. All values presented are means ± 1 SD, unless otherwise stated.

Tracking

During 2012, subsets of the individuals sampled for stable isotope analyses were also tracked using GPS devices (Sirtrack F2, Havelock North, New Zealand [38x11x11mm, 6g]) (see Table 10 for sample sizes). For the incubation and pre-moult trips, devices were deployed before departure and retrieved when the birds returned after 13 days (σ = 1, range = 12-16). To save memory and battery power locations were recorded every 10 minutes. During brood-guard and crèche, deployments lasted for 4 days (σ = 2, range = 2-11), and locations were recorded every 5 minutes. Devices were *c*. 0.2% of the mean adult body mass. As part of the preliminary analysis, data from individuals tracked in 2002 during the crèche phase were also examined (Appendix S12). These birds were tracked using ARGOS satellite-transmitters (Telonics ST10 devices, Mesa, AZ, USA [95 ×42 ×20 mm, 85 g], Sirtrack Kiwisat 10, Havelock North, New Zealand [130×35×20 mm, 100 g] and Wildlife Computers SPOT4, Redmond, WA, USA [90×20×15 mm, 70g]). These instruments were on average <2.25% of the adult mass. Both sets of devices were under the maximum load capacity thought to significantly influence foraging behaviour (Wilson and McMahon 2006). The 2002 study was focused on distribution, and therefore did not involve the systematic blood sampling of tracked individuals. All devices were attached dorsally using waterproof tape (Tesa AG, Hamburg), quick-setting 2-part epoxy glue (RS components, Corby) and cable ties.

The most likely path that a penguin followed and the maximum distance travelled from the colony (km) were derived using the statistical packages *tripEstimation* and *trip*, respectively (Program R; Sumner and Luque 2013; Sumner and Wotherspoon 2013). The

estimated path was constrained by a mean speed of 2 km hr^{-1} with a SD of 1, derived from satellite-tracking of rockhopper penguins *Eudyptes chrysocome* (Reya Rey *et al.* 2007). Observation error was based on the respective error of the GPS device or Argos location class. Time spent at the colony was removed from each deployment based on the location and the saline sensor. A land mask was used to constrain the remaining positions to occur at-sea (derived from the General Bathymetric Chart of the Oceans world coast map, http://www.gebco.net). The *tripEstimation* package uses Bayesian Monte Carlo Markov chains to estimate positions with uncertainly. Five chains of 2000 iterations were simulated, and the initial 500 iterations were discarded as burn-in.

Analysis

The variation in stable isotope ratios due to feather colour (black and white feathers from the same individual) and feather cleaning (cleaned and un-cleaned feathers from the same individual) were examined using mixed models (Zuur *et al.* 2009). The inclusion of individual as a random effect to account for non-independence of observations was tested using a likelihood ratio test. Treatment (colour or cleaning), and in the analysis of colour; sex, and an interaction between sex and treatment were included as fixed effects. Models with different fixed effect structures were compared via stepwise model selection with the Akaike Information Criterion (AIC). Here, more than 2 ΔAIC units was taken to indicate strong support for the model with the lower AIC (Burnham and Anderson 2002). Parameter estimates from selected models were derived using restricted maximum likelihood (REML) estimation (Zuur *et al.* 2009). When investigating the effect of feather cleaning, clusters were identified within the residuals that could not be attributed to the available covariate information (e.g. cleaning, Appendix S13). This violates the assumption that the spread of possible isotopic values is the same within each cleaning treatment (the homogeneity assumption; Zuur *et al.* 2007). Because this analysis was concerned with examining the effect of cleaning only, individuals were manually assigned to clusters in order to control for the unexplained variance ($\delta^{15}N$ >11.25; $\delta^{13}C$ >-20; Appendix S13). This variable was included as a fixed effect alongside cleaning and sex. All analyses were performed in the program R using the statistical packages *nlme* and *RLRsim* (Pinheiro *et al.* 2014; Scheipl and Bolker 2014).

Temporal variation in diet at the population level was examined using samples of the same tissue type collected over time (Appendix S11). Preliminary analysis indicated that $\delta^{13}C$ values differed between years despite birds foraging within a similar maximum distance of

the colony (Appendix S12). To control for yearly fluctuations at the base of the food web, the stable isotope ratios of feathers were standardised to $\bar{x} = 0$ within each year. Because the turnover rate of blood plasma is shorter than each breeding phase, but long enough to provide an integrated dietary record across extended foraging trips, the comparison between tracking data and stable isotope ratios was made using blood plasma. The relationship between individual dietary variation and breeding parameters (timing of breeding and incubation trip duration) was examined using the plasma samples collected at the end of incubation. In line with many previous isotopic studies of diet, initial data exploration was undertaken using linear modelling, with sex and breeding phase as fixed effects (e.g. Wilks MANOVA and ANOVA). However, clear evidence of clustering within the residuals of the best candidate models meant that linear modelling approaches were considered unsuitable for analysing this dataset. Variation among individuals was therefore assessed using multivariate clustering methods to identify potential groupings. Finite Gaussian mixture models were used to assign individual samples to clusters using the combined $\delta^{13}C$ and $\delta^{15}N$ data. For feathers, this analysis considered all years collectively, and for blood cells, blood plasma and guano, all breeding phases collectively. Clusters, hereon referred to as dietary classes, were described as Gaussian kernels with separate variance-covariance structures, and the number of dietary classes within each sample type was determined via the Bayesian Information Criterion (BIC). All analyses were performed in the program R using the statistical package *mclust* (Fraley *et al.* 2014).

To investigate whether the estimated proportion of individuals within each dietary class was conditional on sex, time (year or breeding stage) and breeding parameters multinomial log linear models were used (see Table 11 for model structures). All models included dietary class as the response variable and used stepwise model selection with the second order Akaike Information Criterion (AIC_c). The goodness-of-fit of the best candidate models was quantified by using the model to re-assign data points to a dietary class, and calculating the percentage of individuals correctly identified using a confusion matrix (Matthiopoulos, 2011). All analyses were performed in the program R using the statistical package *nnet* (Ripley *et al.* 2014).

Consistency in an individual's dietary class between years was examined using a randomisation test. The observed probability of specialisation (remaining in the same class) was compared to the expected probability, if assignment had occurred by chance. The observed probability was calculated using black feathers collected from the same

individual before and after moult during the 2012 breeding season (n = 20). The expected probability of specialisation was calculated by pooling data (n = 196) from all 5-years. The proportion of the population within each dietary class for a given year was estimated using conditional probability. For example, if two dietary classes (say, *A* and *B*) are present in each year (T_1, T_2), the probability of consistent membership (M) would be calculated as:

$$P(\mathrm{M}) = P(T_1 = A \cap T_2 = A) + P(T_1 = B \cap T_2 = B)$$

A non-parametric bootstrap selected two sample years from the population distribution and calculated the probability of consistent membership for 10^3 iterations. For each bootstrapped sample, a binomial distribution with probability equal to $P(\mathrm{M})$ and sample size equal to the observed data (n = 20) randomly selected the number of individuals expected to stay within the same dietary class between years. The proportion of bootstrapped samples that estimated the number of individuals consistent in their dietary class between years to be the same as the number observed between 2011 and 2012 was used as a significance test.

Results

Blood plasma samples collected from female macaroni penguins when they first arrived at the colony at the start of the breeding season showed signs of excess lipid (increased C:N ratio; Table 12) possibly associated with the yolk precursor vitellogenin (Crossin *et al.* 2010). These samples were therefore not included in further analysis. The final data set comprised 20 cleaned white feather samples, 16 uncleaned black feather samples, 196 cleaned black feather samples, 102 blood plasma samples, 105 blood cell samples and 50 guano samples (Table 12, Appendix S11).

Effect of feather colour and feather cleaning

White feathers were significantly enriched in ^{13}C (~0.7 ‰; linear mixed model: df=19, t = 18.19, p<0.01) and ^{15}N (~0.4 ‰; linear mixed model: df = 19, t = 9.88, p<0.01) compared to black feathers. The longitudinal sample size was greater for black feathers, so the remaining analyses focused on black feathers only. Sex and an interaction between sex and colour were not retained in this analysis, and there was no evidence for ^{15}N fractionation or ^{13}C enrichment as a result of the cleaning process (Table 13).

Between-individual variation in diet

The finite Gaussian mixture modelling indicated discrete dietary signatures were present across all samples. Two dietary classes were identified in plasma (dietary class 1 and 2; Figure 11A-E), guano (dietary class 3 and 4; Figure 11F-J) and feathers (dietary class 5 and 6; Figure 12), and four discrete classes were identified in blood cells (dietary class 7-10; Figure 11K-O; Figure 13). During each phase of the breeding season, the proportion of individuals within each dietary class was similar in both blood plasma and guano samples; the proportions were also similar in the feather tip samples, which represent the pre-moult period (Figure 13). Whilst the absolute values of the two classes in blood plasma and feather are not the same, within each sample type the difference between them was similar (~2 ‰). The difference between the two classes within guano was slightly larger (~3 ‰). In blood plasma, guano and feather samples dietary classes 1, 3 and 5 was characterised by consistently lower $\delta^{13}C$ values than class 2, 4 and 6 whereas $\delta^{15}N$ values were similar across both classes (Figure 11A-J; Figure 12).

Pre-breeding season

Blood cells collected from individuals shortly after first arrival at the colony were all assigned to a unique group (dietary class 7) that was characterised by lower $\delta^{15}N$ values than those observed in the subsequent breeding season (Figure 11K-O). Based on blood plasma and guano, all individuals were assigned to a single dietary class at arrival (Figure 11A & F; Appendix S11), a signature that was indistinguishable from the depleted ^{13}C grouping also evident during incubation (Figure 11B & G) and pre-moult (Figure 11E & J).

Breeding season

In blood cells, dietary classes 8, 9 and 10 were characterised by $\delta^{13}C$ values that increased throughout the breeding season. The $\delta^{15}N$ values were similar across these classes (Figure 11K-O). Sex-specific dietary classes occurred during crèche: class 9 consisted of males characterised by lower $\delta^{13}C$ values than the females in class 10; the $\delta^{15}N$ values of these classes were comparable (Figure 11N). The composition of dietary classes was best described as a function of sex and breeding phase (Table 11).

Based on feathers (Figure 12), blood plasma and guano (Figure 11E & J), two dietary classes were evident during pre-moult. Results from plasma and guano also indicated that the same two classes were present during incubation (Figure 11B & G; Figure 13), but

during brood guard and crèche, only the enriched ^{13}C grouping was present (Figure 11C-D, H-I; Figure 13). Sex-specific differences were not apparent (Table 11). The composition of dietary classes in blood plasma and guano was associated with breeding phase (Table 11), and there was no evidence that dietary class was related to timing of breeding or incubation duration (Table 14).

Tracking data were obtained from individuals with stable isotope signatures in dietary classes 1 and 2 during the incubation foraging trip (assignment based on blood plasma; Table 10; Figure 14A). The two classes overlapped spatially, but individuals in class 1 travelled approximately 25% (116 km) further along the same orientation than those in class 2 (Table 10). Individuals tracked during brood guard, crèche and pre-moult were all grouped within dietary class 2 (assignment based on blood plasma; Table 10; Figure 14B-D). The maximum distance birds travelled from the colony decreased significantly when central-place constraints were elevated, i.e. during the chick-rearing phases (Table 10). During brood guard and crèche, birds foraged predominantly within the continental shelf zone of South Georgia (Figure 14B-C). Tracks collected the pre-moult period had similar maximum distance measurements to those recorded from class 2 birds tracked during incubation (Figure 14D; Table 10).

Annual variation

The feather isotope data indicated that the level of variation among individuals did not change across the 5-years considered (Figure 13; Table 11). Based on the population data, 55% of individuals were within dietary class 5 and 45% were within dietary class 6 for any given year.

Individual variation in diet

The probability of remaining within the same dietary class during pre-moult was 0.85; 8 individuals stayed within dietary class 5 and 9 individuals stayed within dietary class 6. The remaining 3 individuals moved from class 6 to class 5. The mean probability of maintaining the same dietary class if assignment occurred by chance was estimated from the bootstrapped samples to be $\bar{x} = 0.51$ (σ = 0.01). The proportion of bootstrapped samples that could estimate the same number of individuals displaying a consistent dietary class between years compared to the number observed between 2011 and 2012 was <0.001.

Discussion

The changes in foraging constraints that result from the breeding cycle of the macaroni penguin are, to some extent, a natural experiment for examining how dietary variation changes in relation to seasonality, conspecific density and prey availability at the foraging sites. Here, we show that individuals exhibit highly consistent dietary specialisation through time, and demonstrate that the presence of individual variation is a reflection of seasonal variations in foraging range.

Detection of individual dietary classes using different tissues

Our study shows the value of incorporating sampling of different tissues when evaluating dietary variation using stable isotope approaches. Sample types for which the period of synthesis was shorter than a particular breeding phase (i.e. feathers, blood plasma and guano) were most suitable for examining short-term dietary change. The proportion of individuals within each dietary class obtained from blood plasma and guano were remarkably similar, indicating that the influence of ammonia volatilization on guano samples was highly consistent or negligible. Guano samples thus potentially offer a valuable alternative when examining short-term (i.e. day-to-day) variation in seabird diet because unlike blood sampling, their collection is non-invasive. Furthermore they require less on-site processing when compared to blood, which needs to be centrifuged immediately after collection to successfully separate plasma and cells without the use of anticoagulants (which can affect stable isotope results, Lemons *et al.* 2011). One major drawback of this approach is that obtaining guano samples during handling cannot be guaranteed. Consequently, the sample may not be representative of the wider population. Furthermore, this sample type should not be used to examine diet during extended foraging trips, e.g. during incubation and pre-moult, because samples will only reflect the diet for a day or two prior to return to the colony, which might differ from that during the earlier parts of the trip.

This study also showed that white feathers were enriched significantly in both ^{13}C and ^{15}N compared to black feathers, highlighting the importance of considering differences in levels of pigmentation when interpreting stable isotope ratios in feathers (Michalik *et al.* 2010). The turnover rate of blood cells was longer than an individual breeding phase; therefore they were less effective for examining short-term changes in the diet of individuals during the breeding season. For example, during crèche, ^{13}C was enriched in the blood cells of females compared to males, most likely driven by a switch from pelagic

foraging during incubation to neritic foraging during brood guard (Hobson *et al.* 1994). In contrast, stable isotope ratios in males at crèche will not reflect this change because they were fasting onshore during brood-guard. The sex-specific stable isotope ratios observed during crèche are therefore attributed to specialisation in reproductive roles, and not foraging strategy *per se*. This finding highlights the importance of considering sample type and the temporal scales of interest when analysing the diet of species in which males and females differ in one or more aspects of their breeding behaviour. In contrast to Cherel *et al.*'s (2005) study on king penguins, the blood of male macaroni penguins did not appear to be significantly enriched in ^{15}N following fasting. However, their study examined stable isotope ratios during moult. Although the duration of fasting is similar during brood guard and moult, male macaroni penguins have a higher daily energy expenditure during moult (Green *et al.* 2009) that would likely result in a greater use of endogenous reserves.

Diet during late winter

In comparison to results for the breeding season, individuals did not appear to be employing different dietary strategies to each other during the late winter. In contrast, a study of returning macaroni penguins in the Indian Ocean identified two discrete $\delta^{13}C$ classes in samples of whole blood (Cherel *et al.* 2007). The stable isotope ratios of macaroni penguins upon arrival at South Georgia were more similar to the grouping from the Indian Ocean characterised by lower $\delta^{13}C$ values, which suggests that, like breeding king penguins in that region, the birds had been foraging at the Polar Front (PF) (Cherel and Hobson 2007). Baseline $\delta^{13}C$ is thought to change abruptly across frontal features (Trull and Armand 2001), and the winter distribution of macaroni penguins from Bird Island is concentrated around the Sub-Antarctic Front (SAF), the PF, and the Southern Antarctic Circumpolar Current Front (SACCF; Ratcliffe *et al.* 2014). The range of $\delta^{13}C$ and $\delta^{15}N$ when birds arrived at South Georgia was larger than observed for the individual diet classes during the subsequent breeding season. The lack of discrete groupings may therefore reflect more mixed foraging strategies during the late winter, be an effect of sample size or year, or may reflect birds with more divergent diets and distributions returning to a common geographic area towards the end of winter, resulting in a heterogeneous isotopic signal within individuals. Support for this last hypothesis is that the isotope ratios in blood plasma and guano of recent arrivals were comparable to those obtained for the rest of the breeding season. It is therefore likely that macaroni penguins returned to forage in waters close to the colony for at least a week prior to coming ashore to breed, as also observed in Adélie penguins (Tierney *et al.* 2008).

The $\delta^{15}N$ values of blood cells at arrival indicate that birds were consuming lower trophic level prey during the end of the winter than in the subsequent breeding season. This result was not apparent in macaroni penguins in the Indian Ocean (Cherel *et al.* 2007), but has been observed in some years for Adélie penguins (Tierney *et al.* 2008). During the summer breeding season, ^{15}N is potentially enriched by the inclusion of myctophid fish and other inshore species in the diet that are not available during the winter (Waluda *et al.* 2012). In contrast, during the winter, myctophid fish at the PF are typically distributed lower in the water column (Koslov *et al.* 1991), inaccessible even for deeper-diving king penguins, which migrate to foraging grounds at the marginal ice zone where fish occur at shallower depths (Charrassin *et al.* 2001; Bost *et al.* 2004). In contrast, macaroni penguins remain at the frontal features further north (Ratcliffe *et al.* 2014) and are thus likely to compensate for the lower availability of fish prey by switching to a diet almost entirely composed of crustaceans.

Dietary differences during the breeding season

The synthesis periods for blood plasma, guano and feathers were shorter than the individual breeding phases permitting individual variation in diet to be examined in relation to reproductive constraints. In each of these sample types differences among individuals were evident during the incubation and pre-moult foraging trips (i.e. at the beginning and end of the breeding season), when central place constraints were relaxed and individuals were able to make long foraging trips. During these periods, two discrete $\delta^{13}C$ classes were consistently evident. Consequently, we concluded that in blood plasma, guano and feather samples dietary classes 1, 3 and 5 are likely to represent the same dietary signal (here on referred to as dietary class 1), and likewise for dietary classes 2, 4 and 6 (here on referred to as dietary class 2).

Based on the feather samples, the isotope ratios and proportion of individuals in each of these classes was similar across the five study years; in addition, individuals were highly consistent in their isotopic signature in the two years for which data were available. Despite a large increase in body mass during the incubation and pre-moult foraging trips (Williams 1995), the daily energy expenditure of macaroni penguins when at-sea is no greater during incubation or pre-moult than in the rest of the breeding season (Boyd 2002; Green *et al.* 2009). Birds are thus thought to forage less intensively, perhaps in response to greater resource availability off-shore (Green *et al.* 2009). The acquisition of resources

during these trips will determine an individual's ability to complete the subsequent incubation shift or survive through the moulting period. Birds should therefore forage in locations where prey species were previously encountered with greater frequency or in greater abundance or density. By this action the isotopic signal they acquire should be more distinct in relation to isotope values of prey items eaten in the locations that they foraged.

Blood plasma and guano were collected over multiple breeding stages whereas feathers only represent the pre-moult period. Given the larger sample size of blood plasma, individual variation in diet across breeding phases is discussed below in the context of blood plasma results only. The turnover rate of this sample type means that the signature reflects prey ingested (i.e. the foraging strategy adopted) during a long trip, or the integrated diet signal from several short trips. During incubation, individuals from the two dietary classes appeared to exploit spatially discrete areas. Based on the reduced sample sizes associated with the GPS tags, the class 1 group (n=4, lower $\delta^{13}C$ values) included birds that travelled on average ~25% further from the colony. This additional travel distance took some individuals into waters beyond the PF. During pre-moult, the stable isotope data indicated two dietary classes were present (1 and 2), however all tracked individuals were within dietary class 2 (n=4). The spatial area exploited and distance travelled by these individuals was similar to that shown by birds in class 2 during incubation. In previous years some pre-moult trips were similar to those of class 1 birds during incubation in our study (Waluda *et al.* 2010); we therefore infer that the diets and foraging areas of birds from class 1 and 2 are consistent during the incubation and pre-moult foraging trips, however larger samples sizes of tagged individuals would be needed to confirm this.

The contrasting isotope ratios between the two dietary classes may reflect compositional differences in terms of prey species, or similar prey that are isotopically distinct because they are consumed in two different areas. Although baseline $\delta^{13}C$ is thought to increase north of the PF (Trull and Armand 2001; Cherel and Hobson 2007), in our study the class that included individuals that were tracked beyond the PF had lower $\delta^{13}C$ values. Thus, an alternative explanation is that there is greater ^{13}C enrichment in coastal compared with open ocean ecosystems, a state that is characteristic of marine environments in general (France 1995; France and Peters 1997). Although the continental shelf zone of South Georgia is thought to be depleted in ^{13}C compared to offshore waters (Stowasser *et al.*

2012), cross shelf heterogeneity in $\delta^{13}C$ over short distances (Schell *et al.* 1998) indicates a need for caution when interpreting these gradients. The feather samples considered here indicated that the basal ^{13}C signature of this region can change in different years. This is also suggested by comparing the crèche blood samples examined by Bearhop *et al.* (2006) for 2002 to the crèche blood cell samples reported here for 2012. Multi-year studies examining variation in isotopic baselines and ratios in key prey species would assist with the production of an accurate isoscape for this region, and elucidate the causes of the observed differences in $\delta^{13}C$ between individuals in the two dietary classes during incubation and pre-moult.

Levels of competition are likely to be highest during the chick-rearing phases (brood-guard and crèche) when macaroni penguins and other potential competitors that breed on Bird Island, such as Antarctic fur seals (Reid *et al.* 1996), are all operating under strong central place constraints. Although intra-specific competition is expected to generate selection for between-individual differences in foraging strategies (Stephens and Krebs 1986), inter-specific competition has been linked to a decrease in resource use diversity between conspecifics (Knudsen *et al.* 2007). During chick rearing, all individuals appeared to adopt a single dietary strategy. Foraging ranges are lower during chick rearing than during the incubation and pre-moult periods (Barlow and Croxall 2002a), indicating that individuals are unable to access the foraging locations and resources used at other times that characterise dietary class 1. This reduction in foraging range and resource diversity, potentially coupled with an increase in intra-specific competition, thus appears to force individuals to converge on the same resource.

The presence of discrete dietary classes during the chick-rearing period was suggested previously for females in this population by Bearhop *et al.* (2006). Their study was based on blood cells collected during crèche in 2002. Given the slower turn-over rate of cells than plasma, and hence longer diet integration period, these data were thus likely to reflect individual variation in diet during both crèche and part of the preceding brood-guard phase. Although multiple strategies were not apparent during chick rearing in our study, the degree of specialisation among individuals may vary between years in relation to changes in local prey availability and diversity. Antarctic krill forms a major component of the macaroni penguin diet during the breeding season (Waluda *et al.* 2012), and is advected into the South Georgia region each summer from spawning grounds further south (Murphy *et al.* 1998). Since the life stage and oceanic origin of these krill vary seasonally and

annually, it is quite likely that they may also vary in their isotope ratios (Frazer *et al.* 1997; Schmidt *et al.* 2003; Stowasser *et al.* 2012). We infer that during the Bearhop *et al.* study, female macaroni penguins specialised either on exploiting new immigrants from the south, or older krill from the local standing stock. During 2002, krill density and size diversity increased across this region in comparison to 2012 (Fielding *et al.* 2014). We infer that the degree of individual variation highlighted by Bearhop *et al.* (2006) was in response to greater resource diversity and lower levels of inter-specific competition during their sampling year. In contrast it seems likely that the krill available during chick rearing were more homogenous in their provenance in the 2012 season.

The utilisation of different diets was not related to timing of breeding, incubation trip duration or sex. However, it is notable that the individuals that did shift diets between years (15%) all switched from the inshore strategy (class 1) to the offshore strategy (class 2). Since the majority of birds did not change diets, further work would clarify whether this switch is related to factors such as increasing age and experience, and whether there are any consequences of divergent behaviour in terms of demographic processes.

Conclusion

We show that macaroni penguins consistently employed different foraging strategies when individuals were able to make longer foraging trips. During these periods, birds are thought to increase their daily food consumption despite foraging less intensely (Boyd 2002; Green *et al.* 2009), thus increasing their mass rapidly in preparation for the subsequent fasting periods. The consistency of individual isotopic signatures between years may indicate that birds return repeatedly to locations where prey species were previously encountered with greater frequency or density. There was no difference in lay dates or trip durations between the two dietary classes, suggesting the strategies are largely equivalent strategies in terms of fitness. In contrast, during periods of the breeding cycle with elevated central place constraint, when macaroni penguins and other sympatric predators are concentrated within a restricted range with a limited diversity of potential prey items, birds converged on one strategy. By comparing our results with a previous study, we show that individual dietary variation may also occur during periods with highly restricted ranges, possibly as a product of elevated prey biomass and diversity. We therefore suggest that individual dietary and foraging specialisation occurs in response to resource options, with some degree of plasticity that is likely to buffer population and community-level consequences.

Table 8. The breeding cycle of macaroni penguins at Bird Island, South Georgia with timing of stable isotope sample collection (adapted from Williams 1995; Barlow and Croxall 2002a; Green *et al.* 2009). * sampling period; † period of on-shore fasting.

Month	Sampling interval	Trip durations	Male		Female	
			Breeding duty	Body mass (% change)	Breeding duty	Body mass (% change)
October	*Start of breeding season*		Courts†	-	Courts†	-
November	Incubation	12-14 d	Incubates†	- (30)	Incubates†	-
			At-sea*	+ (40-50)	Incubates†	- (40)
December	Incubation	9-11 d	Incubates†	-	At-sea*	+ (30)
January	Brood guard	11-12 hr	Brood guard†	- (40-50)	Provisions*	- (20)
	Crèche	11-50 hr	Provisions*	+ (20)	Provisions*	- (10)
February	Pre-moult	12-14 d	At sea*	+ (50-70)	At sea*	+ (40-60)
March			Moults†	- (50)	Moults†	- (50)
April	*End of breeding season*		At sea	+	At sea	+

Table 9. Timing of breeding (laying date) and incubation trip duration of macaroni penguins at Bird Island, South Georgia, in relation to assigned dietary class based on plasma samples collected during incubation (see Figure 14A for spatial distribution).

	Total n			
	Class 1	Class 2	Class 1	Class 2
Laying date of b-egg (days since 1 November)	16	6	18.25 ±2.35	17.83 ±2.04
Trip duration (days)	16	6	11.88 ±2.16	11.50 ±3.02

Table 10. The number of macaroni penguins tracked from Bird Island, South Georgia, and maximum distance travelled during the 2012 breeding season by breeding phase and assigned to dietary classes. Individuals were assigned to dietary classes based on stable isotope ratios in blood plasma.

Breeding phase	*Total n*		*Total n*				Maximum distance from the colony (km)	
	M	F	M	F	M	F		
			Class 1		Class 2		Class 1	Class 2
Incubation	3	6	3	1	0	5	476 ±82	360 ±52
Brood	-	14	-	0	-	14	-	23 ±19
Crèche	5	6	0	0	5	6	-	22 ±35
Pre-moult	2	2	0	0	2	2	-	357 ±40

Table 11. Factors influencing population-level specialisation of dietary class over different time periods for macaroni penguins from Bird Island, South Georgia. Goodness of fit (GOF) shown for best candidate model. Notation; (.) intercept only model, (S) sex, (P) breeding phase, (Y_f) year as a factor, (Y_n) year as a continuous variable

Tissue	Model	GOF	df	AIC_c	ΔAIC_c
Feathers	.	55.1	1	271.7	0.00
	S		2	271.9	0.25
	Y_n		2	272.2	0.56
	$S + Y_n$		3	272.5	0.81
	Y_f		5	276.2	4.54
	$Y_f + Y_n$		5	276.2	4.54
	$S + Y_f + Y_n$		6	276.5	4.82
	$S + Y_f$		6	276.5	4.82
Blood plasma	P	80.4	5	77.9	0.00
	S + P		6	77.9	0.06
	S * P		8	79.0	1.17
	S		2	135.6	57.72
	.		1	140.2	62.38
Guano	P	90.0	5	33.3	0.00
	S + P		6	35.8	2.58
	S * P		9	44.4	11.12
	S		2	65.3	32.08
	.		1	71.3	38.06
Blood cells	S + P	79.1	18	128.1	0.00
	P		15	140.7	12.61
	S * P		27	146.8	18.68
	.		3	276.5	148.36
	S		6	279.4	151.25

Table 12. Stable isotope signatures of macaroni penguins from Bird Island, South Georgia, by sex and time (year or breeding phase). Values are mean ±1 standard deviation. Notation; *n* total sample size, (W) winter, (Inc) incubation, (BG) brood guard (female only), (Cr) crèche, and (PM) pre-moult, (M) male, (F) female. * Samples removed because of increased atomic C:N ratio.

Sample	Year	Phase	*n*	$\delta^{13}C$		$\delta^{15}N$		C:N	
				M	F	M	F	M	F
Feather	2001	PM	40	-21.4 ±0.8	-21.4 ±0.7	9.5 ±0.6	9.3 ±0.7	3.7 ±0.0	3.7 ±0.0
	2002		40	-19.7 ±1.2	-19.9 ±1.0	11.5 ±0.5	10.9 ±0.7	3.8 ±0.0	3.8 ±0.0
	2003		33	-20.9 ±1.3	-21.2 ±1.1	10.9 ±0.5	10.7 ±0.5	3.8 ±0.0	3.8 ±0.0
	2011		42	-21.2 ±1.2	-21.4 ±1.0	10.9 ±0.5	10.8 ±0.4	3.8 ±0.0	3.8 ±0.0
	2012		41	-21.2 ±0.7	-21.4 ±0.7	10.6 ±0.4	10.4 ±0.3	3.8 ±0.0	3.8 ±0.0
Blood Plasma	2012	W	12	-24.5 ±0.3	-26.1 ±1.3	9.7 ±0.3	9.1 ±0.5	5.4 ±0.4	9.3 ±3.1*
		Inc	22	-24.1 ±0.5	-23.4 ±0.8	9.7 ±0.3	10.1 ±0.3	5.2 ±0.2	5.3 ±0.1
		BG	9	-	-21.9 ±0.2	-	10.3 ±0.6	-	5.4 ±0.2
		Cr	29	-21.9 ±0.4	-21.7 ±0.3	9.3 ±0.2	9.4 ±0.4	5.2 ±0.2	5.3 ±0.2
		PM	30	-23.0 ±1.1	-22.9 ±1.0	10.0 ±0.3	10.2 ±0.2	5.0 ±0.2	5.1 ±0.3
Guano	2012	W	10	-25.4 ±0.5	-24.9 ±0.1	6.4 ±1.0	5.6 ±0.9	2.0 ±0.7	1.9 ±0.3
		Inc	8	-25.4 ±0.8	-24.5 ±1.2	6.0 ±1.5	6.6 ±0.9	2.8 ±1.7	1.3 ±0.0
		BG	9	-	-22.1 ±0.9	-	6.7 ±1.2	-	2.5 ±1.1
		Cr	12	-22.0 ±1.0	-21.9 ±0.7	6.0 ±1.2	4.6 ±1.2	2.7 ±1.4	3.0 ±1.7
		PM	11	-24.8 ±0.8	-25.2 ±1.0	5.7 ±1.3	5.5 ±1.7	2.3 ±1.0	2.2 ±1.4
Blood cells	2012	W	20	-22.4 ±0.3	-22.4 ±0.5	7.8 ±0.5	7.7 ±0.4	3.8 ±0.0	3.4 ±0.0
		Inc	22	-22.9 ±0.2	-22.2 ±0.5	9.4 ±0.2	9.6 ±0.3	3.8 ±0.0	3.8 ±0.1
		BG	9	-	-21.8 ±0.4	-	9.9 ±0.3	-	3.8 ±0.0
		Cr	22	-21.6 ±0.3	-20.9 ±0.5	9.8 ±0.3	9.5 ±0.3	3.8 ±0.0	3.8 ±0.0
		PM	27	-21.0 ±0.6	-20.9 ±0.5	9.5 ±0.4	9.4 ±0.3	3.8 ±0.0	3.8 ±0.0

Table 13. Influence of feather colour and chloroform: methanol cleaning on the stable isotope signature for samples collected from macaroni penguins at Bird Island, South Georgia. Notation; (.) intercept only model, (S) sex, (C) colour, (R) chloroform: methanol cleaning rinse, (G) cluster grouping.

Treatment	Isotope	Model	df	AIC_c	ΔAIC_c
Colour	$\delta^{13}C$	C	4	55.3	0.00
		C + S	5	57.2	1.92
		C * S	6	59.5	4.25
		.	3	111.1	55.78
		S	4	112.8	57.55
	$\delta^{15}N$	C	4	8.6	0.00
		C + S	5	9.8	1.28
		C * S	6	11.0	2.40
		.	3	42.4	33.83
		S	4	44.6	36.08
Cleaning	$\delta^{13}C$	R + G	5	-4.6	0.00
		G	4	-1.8	2.88
		R	4	28.0	32.58
		.	3	31.0	35.66
	$\delta^{15}N$	G	4	-6.5	0.00
		R + G	5	-3.7	2.80
		.	3	20.9	27.41
		R	4	23.5	30.01

Table 14. Influence of breeding parameters (timing of breeding and incubation trip duration) on dietary class assignment within incubation using blood plasma samples collected from macaroni penguins at Bird Island, South Georgia, during the 2012 breeding season. Goodness of fit (GOF) shown for best candidate model. Notation; (.) intercept only model, (S) Sex, (L) timing of breeding (laying date for b-egg), and (T) incubation trip duration.

Model	GOF	df	AIC_c	ΔAIC_c
S		2	23.1	0.00
.	72.2	1	23.5	0.47
S + T		3	24.5	1.47
S + L		3	25.3	2.23
L		2	25.8	2.75
T		2	25.9	2.88
L + S + T		4	26.1	3.08
L + T		3	28.5	5.46

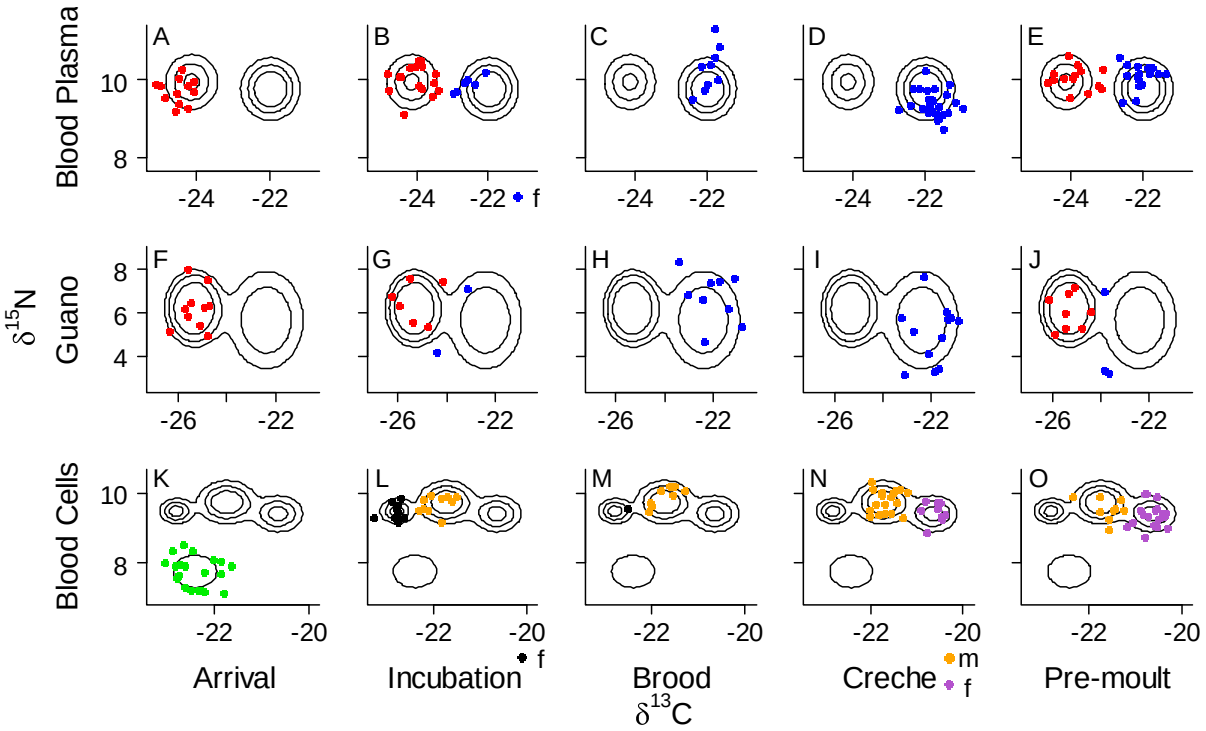


Figure 11. Stable isotope ratios of macaroni penguins sampled at Bird Island, South Georgia, A-E) blood plasma showing two distinct dietary classes class 1 (red) and class 2 (blue); F-J) guano showing two distinct dietary classes class 3 (red) and class 4 (blue) and K-O) blood cells showing four distinct dietary classes in figures K-O: class 7 (green), class 8 (black), class 9 (orange), and class 10 (purple). Sex-specific clusters are indicated beneath the x-axis if they occurred when samples from both sexes were considered (i.e. not during brood guard); (m) male, (f) female. Density contours shown for total data set at 0.25, 0.5 and 0.75.

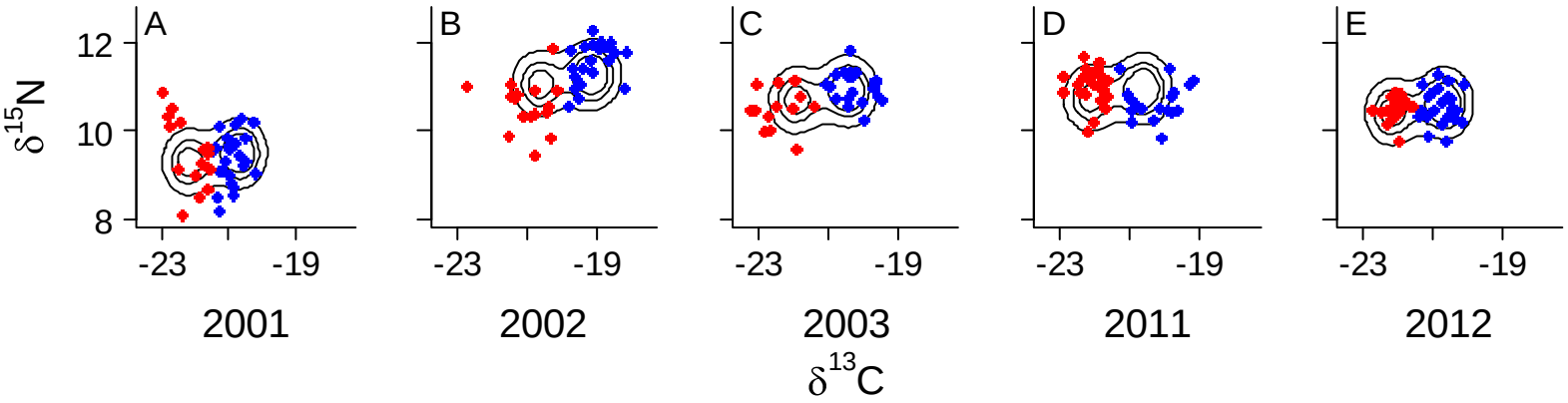


Figure 12. Stable isotope ratios of black feathers of macaroni penguins sampled at Bird Island, South Georgia, showing two distinct dietary classes: class 5 (red) and class 6 (blue). Data points shown as de-standardised. Density contours shown for total data set at 0.25, 0.5 and 0.75.

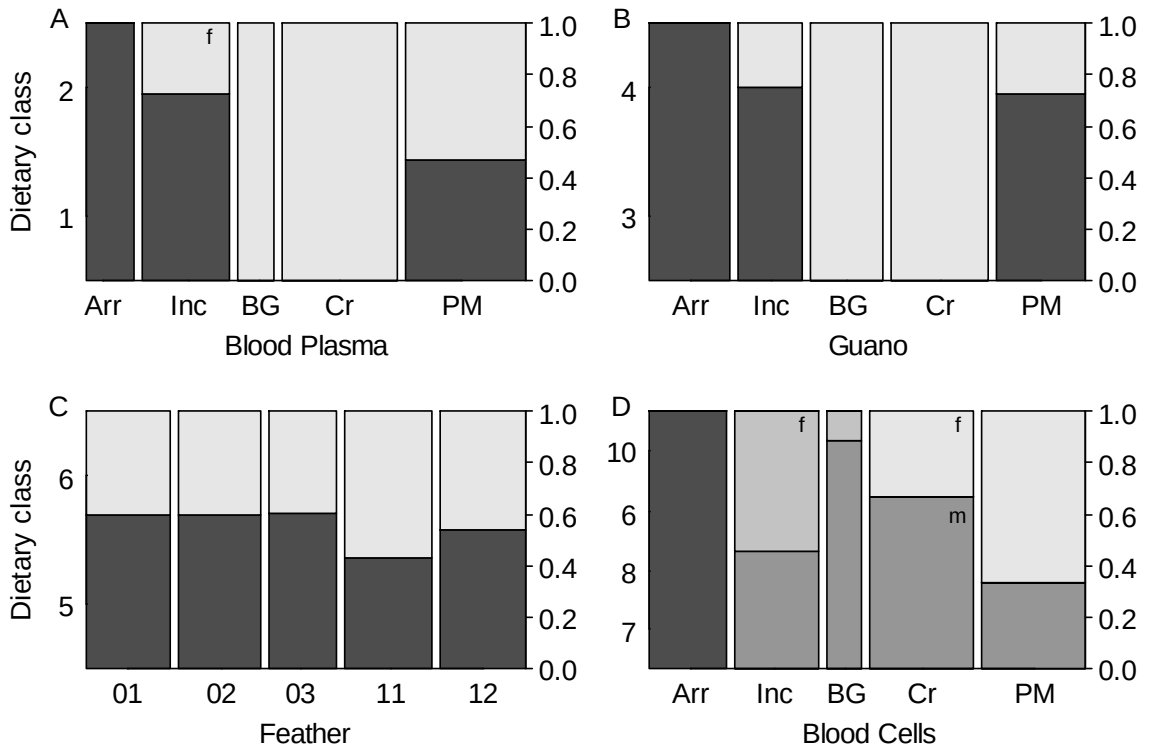


Figure 13. Proportion of macaroni penguins sampled at Bird Island, South Georgia, within each dietary class for A) feathers by year; B) blood cells by breeding phase during the 2012 breeding season; C) blood plasma by breeding phase during the 2012 breeding season; and D) guano by breeding phase during the 2012 breeding season. Colours of dietary classes indicated on the x-axis. Notation; (Arr) arrival, (Inc) incubation, (BG) brood guard (female only), (Cr) crèche, and (PM) pre-moult. Sex-specific clusters are indicated if they occurred during time periods when samples from both sexes were considered; (m) male, (f) female. Column widths are proportional to the number of samples considered (Table 10; Appendix S11).

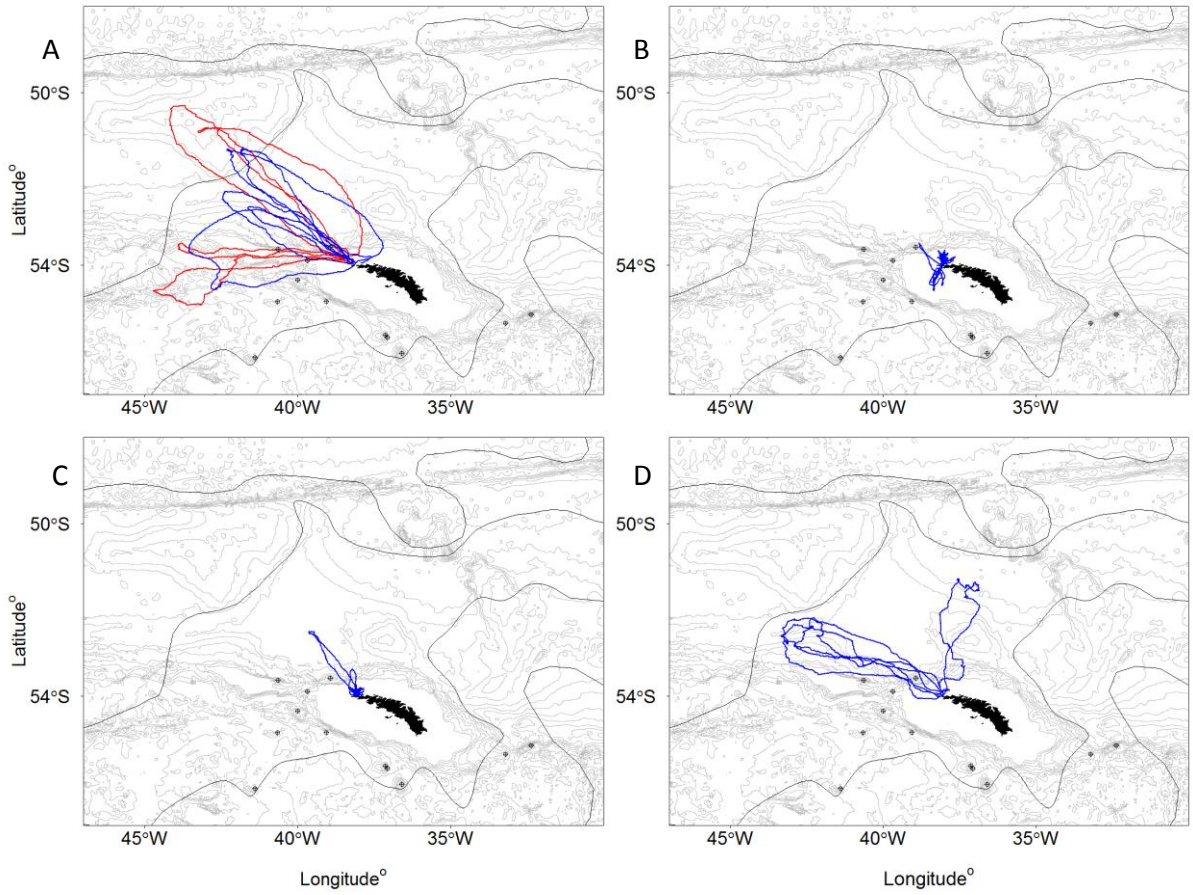


Figure 14. GPS tracks from macaroni penguins in the 2012 breeding season classified on the basis of stable isotope ratios in blood plasma as dietary class 1 (red) and dietary class 2 (blue) during A) incubation; B) brood guard; C) crèche; and D) pre-moult. Average position of ocean fronts following black lines; top down: SAF - Sub-Antarctic Front; PF - Polar Front; SACCF - Southern Antarctic Circumpolar Current Front, and SACCB - Southern Antarctic Circumpolar Current Boundary. The general pattern of the surface current flow in the Scotia Sea is from west to east in line with the major ocean fronts. The study area, Bird Island, is at the western end of South Georgia. Bathymetry contours (grey lines) every 500m, and seamounts shown with crosshairs.

Chapter 7

General Discussion

A major focus in population ecology is to understand the relative importance of top-down and bottom-up forces on demographic parameters (Hunter and Price 1992; Roughgarden *et al.* 1994). In this thesis I have examined the demography and population dynamics of a declining population of macaroni penguins (*Eudyptes chrysolophus*) in order to identify the drivers of year-to-year variation and quantify their influence. The aims were realised by capitalising on relatively recent methodological advances in the collection of mark-recapture data (Green *et al.* 2006), population modelling approaches (Durbin and Koopman 2001; Buckland *et al.* 2004), diet quantification (Cherel and Hobson 2007) and animal telemetry (Ropert-Coudert and Wilson 2005).

This thesis was also dependent on the long-term monitoring data collected on macaroni penguins breeding at Bird Island, South Georgia. The monitoring of population size and productivity since 1985 and the high-resolution mark-recapture data collected since 2003 permitted the key processes that influence demographic rates to be examined (Chapter 3; Chapter 4; Chapter 5). Furthermore, the plethora of short-term studies that have been undertaken using macaroni penguins from Fairy Point provided information to assist with interpretation. Finally, archived tracking data and feather samples allowed the fieldwork carried out in 2012 to be investigated in a wider temporal context (Chapter 6). The intention of this chapter is to draw together the wider implications of the work, and to set priorities for future research.

Main findings

The principal aims of this study that are outlined in Chapter 1, can be posed as a series of research questions, the concise answers to which summarise the main findings:

1. What are the principal drivers of year-to-year variation in the survival rates of macaroni penguins between 2003 and 2012?

Analysis was carried out using recapture data collected across 10 years. Over this time 1070 macaroni penguins were PIT tagged at fledging and 966 individuals were PIT tagged at age 1 or above (Chapter 3). Survival rates were best described in two age-classes that were low and variable during the fledging year ($\bar{x} = 0.33, \sigma = 0.12$), increasing from age 1 onwards ($\bar{x} = 0.89, \sigma = 0.01$) (Figure 5). There was no evidence for an effect of sex (Chapter 4). Chapter 3 represents one of the first studies to illustrate how penguin survival rates may change under different levels of top-down control. A negative association with predation pressure from giant petrels was indicated for both age classes, albeit to a much lesser extent for birds older than age 1. The survival rates of both age classes were also positively associated with sea surface temperature. Whilst the majority of penguin climate-demography studies report a negative association between survival rates and climate warming, a positive effect has also been noted in two other species (Sidhu *et al.* 2012; Saraux *et al.* 2011b). It is possible that optimum extrinsic conditions may exist regionally, such that relationships between survival and environmental effects are nonlinear and possibly non-monotonic. The observed trend with warming will thus depend on whether the conditions at the study location are above or below the optimum. Finally, in agreement with previous work on other penguin species (Olsson 1997; McClung *et al.* 2004), macaroni penguins fledging with heavier body masses had consistently higher survival rates than birds that fledged lighter within a given year. Years with low fledging masses and survival rates coincided with a change in the principal prey species (Waluda *et al.* 2012). Bottom-up control associated with a change in food supply is thus the most obvious driver during these years.

2. What is the relative importance of the different drivers that influence the survival rates of macaroni penguins?

I used a sensitivity analysis to assess the relative importance of each driver in determining the survival rates of macaroni penguins (Chapter 3). The relative importance was age specific. During the fledging year, survival rates were most sensitive to top-down predation pressure, followed by individual fledging mass, and finally bottom-up environmental effects. Lacking in experience, size and strength, fledgling birds are considerably more susceptible to predation than adult birds. In contrast, birds older than age 1 showed a

similar response to bottom-up and top-down control (Table 4). The age-specific response of macaroni penguins to the physical and biological processes considered here confirms the importance of considering multiple causal effects across different life stages when examining the survival rates of seabirds.

3. How do the survival rates estimated in Chapter 3 for the period of population stability between 2003 and 2012, compare to survival rates estimated for the period of population decline between 1985 and 2012?

In order to hind-cast the missing segments of the time series for survival rates I used an age-structured state-space population model. This approach combined the 28-year time series of population counts and productivity measurements with the 10-year time series of survival rates estimated in Chapter 3 to model the missing values as a function of the covariates (Chapter 5). The survival rates of both age classes increased between 1985 and 2012. Whilst the overall average values were similar to the rates estimated in Chapter 3, year-to-year variability was considerably greater during the period of population decline. Mean survival rates across the whole study period for the fledgling age class were $\bar{x} = 0.40$ ($\sigma = 0.19$), and for the older age class were $\bar{x} = 0.87$ ($\sigma = 0.04$) (Chapter 5; Figure 9). There were also three large mortality events between 1985 and 2000 that were inferred to be associated with elevated levels of predation pressure.

4. What are the principal drivers of year-to-year variation in the productivity rates of macaroni penguins between 1985 and 2012?

The integrated population model showed that year-to-year variation in productivity was best described as a function of pre-breeding condition, the El Niño Southern Oscillation, predation pressure and population size. The mean productivity rates reported in Chapter 5 were similar to the rates reported for other decreasing populations of macaroni penguins with comparable numbers of breeding pairs ($\bar{x} = 0.46 - 0.57$ chicks pair^{-1}; Crawford *et al.* 2006). However, productivity increased during the study period, and by 2012, rates were similar to those reported for increasing populations of southern rockhopper penguins ($\bar{x} = 0.64$ chicks pair^{-1}; Baylis *et al.* 2013). Fluctuations in pre-breeding condition may be driven by conditions at winter foraging grounds, however macaroni penguins probably return to forage in waters close to the colony for at least a week prior to coming ashore to breed (Chapter 6). Pre-breeding condition may thus reflect conditions more local to the

colony. ENSO is thought to change the environmental carrying capacity of this ecosystem, and in agreement with other penguin-demography studies this analysis suggested that productivity decreased during El Niño events, possibly indicating that intra-specific competition dominated food availability in these years. However, the effect of ENSO did not appear to change in relation to population size indicating that El Niño events created elevated levels of intra-specific competition even at lower population densities. This may reflect a change in the carrying capacity of the breeding season environment over the study period (Agnew 2004; Atkinson *et al.* 2004), or alternatively a change in the nature of El Niño events since the late 1970s (Ashok *et al.* 2007). Finally, the positive association between predation pressure and productivity is likely to reflect an environmental effect that is favouring both species during the chick-rearing phases. The increase in productivity could not be attributed to changes in ENSO, pre-breeding condition or predation (Chapter 2, Chapter 5), but appeared to be associated with reduced levels of intra-specific competition owing to the population decline.

5. What is the relative importance of different drivers influencing the population trajectory of macaroni penguins between 1985 and 2012?

The breeding population of macaroni penguins at Bird Island declined at 6% (SE=0.01) per year between 1985 and *c.* 2000. The population trajectory then potentially stabilised (Figure 8). During the period of population decline recruitment was lower than adult mortality, and three large mortality events occurred (1986, 1987 and 1994; Figure 9A). The population trajectory was most sensitive to the influence of predation pressure on survival rates, where the relationship with birds older than age one was considerably more influential than with fledgling birds (Table 7). All other covariates were significantly less influential. It therefore appears that the population declined in response to lower survival and productivity rates, but that this trend was accelerated by three large mortality events that occurred in associated with elevated levels of top-down predation pressure. The population trajectory later stabilised in response to survival and productivity rates increasing. The mechanism causing survival rates to increase was not identified in this study due to the methodological limitations of formal model selection within the state-space framework. The increase in productivity was attributed to density-dependence feedbacks with the declining population. The future stability of this population will thus depend on the carrying capacity of the environment supporting productivity rates at their

present level, in addition to the population size and breeding success of giant petrels not increasing so that adult survival rates can remain stable.

6. Does spatial and seasonal heterogeneity in resources affect the dietary decisions of breeding macaroni penguins?

Analysis of 489 stable isotope samples collected over 5 years indicated that inter-individual differences in diet occur at the beginning and end of the breeding season, i.e. during the incubation and pre-moult foraging trips (Chapter 6). During these phases of the breeding season central place constraints are relaxed in order to enable individuals to make long foraging trips in preparation for the subsequent incubation or moulting fasts. During these periods two discrete $\delta^{13}C$ classes were evident. GPS tracking data collected from 38 individuals across the breeding season indicated that these classes were spatially distinct (Chapter 6). In contrast, during chick rearing, dietary strategies were homogenous. At this time macaroni penguins and other colonially breeding species on Bird Island are concentrated within a restricted foraging range. Levels of competition are therefore likely to be highest during these phases. The reduction in foraging range and resource diversity, coupled with an increase in intra-specific competition, thus appears to have forced individuals to converge onto the same resource at this time.

7. Are individuals specialised in their dietary choices between years?

Feather samples collected from the same individual in two consecutive years showed that individuals were highly consistent in their dietary class during the pre-moult foraging trip. The acquisition of resources during these trips will determine an individual's ability to survive through the moulting period. The adoption of a particular foraging strategy by an individual may optimise its daily energy expenditure, and reduce the overall level of intra-specific competition. By comparing our results with a previous study, it also appears that individuals may adopt discrete dietary strategies during the chick-rearing periods of the breeding season when highly restricted ranges occur, possibly in response to elevated levels of resource diversity (Bearhop *et al.* 2006; Fielding *et al.* 2014; Chapter 6).

Implications of thesis findings

Physical processes and nutrient fluxes dominate the structure and functioning of the open ocean (Behrenfeld *et al.* 2006). The prevailing view is therefore that top-down regulation

in this system is unlikely, and most population change in the open ocean, apart from those resulting from human exploitation, is thought to result from nutrient-driven or "bottom-up" control (Aebischer *et al.* 1990; Stenseth *et al.* 2002). The early view was that Antarctic and Sub-Antarctic oceanic systems were relatively simple; characterised by a large prey resource supporting an assemblage of apex predators (Laws 1977). In Chapter 3, mark-recapture modelling approaches were used to demonstrate the influence of individual traits, bottom-up and top-down processes on survival rates. This is the first seabird demography study to consider these processes simultaneously in order to assess their relative importance to this demographic process. This chapter also provides the first robust estimates of age-specific survival rates in macaroni penguins. Furthermore, the findings add to a limited number of studies to have indicated that demographic processes of polar "apex" predators can be driven from both the bottom-up and the top-down (Reid *et al.* 2013; Schwarz *et al.* 2013). Thus, food web pathways may also occur between particular polar predators. By re-evaluating these species as mid-trophic level consumers we are required to consider the impact of multiple drivers when examining their population dynamics.

Croxall and Rothery (1991) and Nur and Sydeman (2000) proposed that density independent factors may keep certain seabird populations below the levels that density-dependent factors act. The integrated population model outlined in Chapter 5 utilised the drivers of survival rates identified in Chapter 3 and Chapter 4 to investigate this. The findings indicate that this population may have experienced influential density-dependent regulation between 1985 and 2000. In this instance, the increase in productivity as the population declined is one of the mechanisms thought to have stabilised the population trajectory at *c*. 2000. However, the population trajectory was considerably more sensitive to changes in survival rates associated with predation pressure than any of the other covariates considered. It appears that the population declined in response to recruitment being on average lower than adult mortality between 1985 and 2000. This rate of decline was further accelerated by three large mortality events that were associated with high levels of giant petrel predation. An examination of the demography of other species breeding on Bird Island, suggests that some form of combined resource (bottom-up) and predatory (top-down) control is operating during these years (Williams and Rodwell 1992; Reid and Croxall 2001).

In Chapter 6, stable isotope and tracking analysis were combined to investigate the within-individual strategies macaroni penguins might employ to mitigate the impacts of intra-specific competition during the breeding season. Temporal variation in dietary specialisation was examined as a function of sex, breeding parameters and foraging constraints. These findings provide a new perspective on the way macaroni penguins utilise available resources when under central place constraint. They also offer further explanation to previous studies that have found discrete dietary groupings to be present within this population, and provide one of the first insights into the diet of macaroni penguins during the winter. As birds are fully pelagic during this stage, it is only by using techniques such as stable isotope analysis that dietary variation can be resolved over this timescale. This analysis indicated that birds were potentially consuming lower trophic level prey during the end of the winter than in the subsequent breeding season. During the summer breeding season, birds may include fish and other inshore species in the diet that are not available during the winter. Fish may thus be a less important component of the diet during the inter-breeding period than previously suspected. In contrast, the increase in $\delta^{15}N$ at the beginning of the breeding season may indicate that fish forms a more important part of the general breeding season diet than previously thought based on stomach content analysis.

The long-term population trend of macaroni penguins

This thesis has described the processes underpinning the population trajectory of macaroni penguins at Bird Island, South Georgia, between 1985 and 2012, however it is also notable that prior to 1985 this population experienced rapid population growth rates (*c.* 500% between 1958 and 1977; Croxall and Prince 1979; Figure 1). It therefore appears that during the mid-1900s productivity and/or survival must have been consistently within, or above, the upper extent of the rates reported here. Based on the findings and interpretation in this thesis, I offer the following hypotheses as a short review on the possible mechanisms that may have caused the shift in demographic rates that occurred prior to the study period considered here. Although these theories are presented as separate categories, note that they can also overlap: 1. competition with conspecifics, and recovering populations of Antarctic fur seals, whales and elephant seals following the cessation of their harvesting (Table 1; Figure 1); 2. competition with regional fisheries (Table 1; Figure 1; Figure 2); and 3. increased levels of predation.

1. The population trajectory of macaroni penguins on South Georgia rapidly decreased between the 1970s and 2010s (Trathan *et al.* 2012). This was especially apparent at colonies in the western region, i.e. at Bird Island (Trathan *et al.* 2012). However, a number of smaller populations, particularly those in the east continued to increase over the same period (Trathan *et al.* 2012). Being downstream of Bird Island, the eastern colonies receive the seasonal influx of krill first and there is a significant depletion effect as the krill is advected around South Georgia from east to west during the breeding season (Brierley *et al.* 2002). At lower conspecific densities these colonies may thus experience higher per capita food availability than colonies in the west. Further work is needed to understand why these eastern colonies did not reach the carrying capacity of the environment at the same time as the Bird Island population considered in this thesis.

One possible explanation may be levels of inter-specific competition. At South Georgia, the breeding season foraging grounds and diets of macaroni penguins and Antarctic fur seals strongly overlap (Reid *et al.* 1996). The population trajectories of these two species between 1950 and 2010 are also highly similar, although the rates of decline were significantly greater for penguins (Forcada and Hoffman 2014; Chapter 5). It therefore seems highly likely that the colony of macaroni penguins at Bird Island was influenced by competition during the study period considered here, but that fur seals were less impacted. An alternative competitor is elephant seals. Although recorded to predate on myctophid fish in the Indian Ocean (Cherel *et al.* 2008) and krill in the Pacific Ocean (Walters *et al.* 2014), elephant seals breeding at South Georgia are thought to mainly target squid (Rodhouse *et al.* 1992). This makes them an unlikely competitor with macaroni penguins for prey resources during the breeding season. Furthermore, between 1965 and 1995 the population of elephant seals at South Georgia is not thought to have changed size, despite harvesting being stopped in 1965 (Boyd *et al.* 1996). In contrast, certain species of whales have recovered throughout the Southern Ocean (Clapham *et al.* 1999). Competition with whales could result in reduced population survival for macaroni penguins. However, the survival rates of macaroni penguins increased over the study period, alongside the recovery of certain whale stocks. It therefore appears that competition with whales is also unlikely. Furthermore, the proportion of the estimated krill biomass within the Scotia Sea and Antarctic Peninsula region consumed by whales during the summer months is relatively low (4-6%; Reilly *et al.* 2004).

2. In an average year, the diet of macaroni penguins during the breeding season is dominated by fish and krill (Waluda *et al.* 2012; Chapter 6). Major fishing efforts occurred at South Georgia during the 1970s and 1980s (Chapter 2; Table 1; Figure 1; Figure 2). The large catches reported during this period may reflect an increase in the populations of krill-eating fish in response to the krill surplus. However, fish stocks are known to have been overexploited (Kock 1992; Agnew 2004) and their recovery following the closure of specific fisheries is not well understood (Kock 1992). A lack of recovery has been reported in some species of finfish (Chapter 2) that may reflect less of their target prey species (i.e. krill) in the system. An alternative explanation is that levels of predation pressure from penguins, seals or other fish species at different life stages are limiting the population growth of these fish stocks. This mechanism has been observed in other species (e.g. Boveng *et al.* 1998; Frank *et al.* 2005). Chapter 6 indicates that fish may form a more important part of the general breeding season diet of macaroni penguins than previously thought, however further work is needed to understand how dependent macaroni penguins are upon fish species during this period.

Krill was first targeted by a small fishery in the 1960s, but full-scale commercial operations commenced in the mid-1970s (McElroy 1984). The fishery was unregulated until 1992 when a total allowable catch was introduced (CCAMLR 1989-2013). Prior to this, up to 20% of the standing stock at South Georgia was removed each year ($3x10^5$ tonnes; Figure 2). In the early 1980s the standing stock of krill was estimated to be in the order of 1.5 million tonnes (Trathan *et al.* 1995). Based on a full-krill diet, macaroni penguins at South Georgia are estimated to consume 8.08 million tonnes annually (Boyd 2002). Thus, a high rate of krill influx into the region is required in order to sustain these populations alongside other krill-dependent species during the summer breeding season (Croxall *et al.* 1984; Trathan *et al.* 1995; Boyd 2002). The krill influx follows the retreat of sea-ice further south and peaks in the middle of summer. This can be seen in the reduction in carapace length present in fur seal scats over the breeding season (Reid *et al.* 1996). The influx of krill each summer from spawning grounds further south (Siegel *et al.* 1988) should mean that the fishery had a negligible effect on the overall krill biomass at South Georgia during the late summer. However, as macaroni penguins may return to forage in waters close to the colony for at least a week prior to coming ashore to breed (Chapter 6), and pre-breeding condition can influence population productivity (Chapter 5), the standing stock of prey species at South Georgia, including krill, may form an essential part of the early breeding season diet for macaroni penguins. The importance of the standing stock is

likely to be amplified during years where the influx of krill is low. During the summer months the foraging range of macaroni penguins is restricted to an area around the breeding colony; significant levels of competition with regional fisheries during the 1970s and 1980s could therefore have resulted in reduced population productivity (e.g. Mangel and Switzer 1998). Further work is needed to elucidate the relative importance of krill predators, the krill fishery operating during the winter months, as well as emigration of krill due to advection in driving krill density and biomass at South Georgia.

3. We have seen that predation by giant petrels can influence the survival rates of macaroni penguins (Chapter 3). However, there are also near-shore observations of otariid species (Bonner and Hunter 1982; Lalas *et al.* 2007), Leopard seals (Walker *et al.* 1998) and killer whales (Pitman and Durban 2010) predating on various species of penguin. Because of the difficulties in observing this behaviour at-sea where it usually occurs, little is known about their influence on macaroni penguins during both the breeding and inter-breeding period. For the demographic rates of macaroni penguins to have shifted between 1977 and the start of this study in 1985, predation levels from one or all of these species would have had to increase abruptly during this time.

Populations of the two giant petrel species increased at Bird Island between 1979 and 1996 (González-Solís *et al.* 2000). This has been attributed to the increase in fur seal populations producing more carrion during the chick-rearing stages of their breeding season (González-Solís *et al.* 2000). However, the breeding season diet of giant petrels at this time was documented to have been dominated by adult macaroni penguins (Hunter 1983). Thus population growth of giant petrels may also reflect the increase in penguin populations between the 1950s and 1970s. The continued increase in giant petrel populations between 1985 and 2000, when macaroni penguin populations were decreasing, does however suggest that these populations were not reliant on penguins as a prey resource. An alternative explanation is that penguin populations did not fall below a threshold that would impact giant petrel productivity.

The population of fur seals at Bird Island started declining in the 1990s at a slower rate than macaroni penguins (Forcada and Hoffman 2014; Figure 1; Figure 8). The weaning mass of fur seal pups also declined during the same period (Forcada and Hoffman 2014). Macaroni penguins and Antarctic fur seals largely target the same prey species and foraging areas (Reid *et al.* 1996; Barlow *et al.* 2002). Thus, if density dependence effects

contributed to the drop in macaroni penguin productivity, it is also likely to have influenced the demographic rates of fur seals. At Bird Island, fur seals have been documented to predate on macaroni penguins during the breeding season (Bonner and Hunter 1982; pers. obs.). If lower fish and krill stocks were available to macaroni penguins and fur seals during the 1970s and 1980s, the lag between the points of population change for these two species may reflect fur seals outcompeting penguins for available krill and fish, but could also reflect fur seals increasing their levels of predation on macaroni penguins. If predation was an influential driver of penguin population change, one would expect, as observed, levels of penguin survival to increase as the population of fur seals started declining in the early 1990s (Figure 9; Forcada and Hoffman 2014). This hypothesis would not stand if predation of penguins by fur seals is carried out by a limited number of specialist individuals, because this is unlikely to be related to population size. Additional work examining whether a historic switch in dietary preference of fur seals may help elucidate this.

Finally, leopard seals are present at Bird Island during the austral winter. Thus predation on macaroni penguins at Bird Island is only possible at the beginning of the macaroni penguin breeding season (Walker *et al.* 1998). As giant petrels can exert top-down control on macaroni penguins by predating during the narrow temporal window of fledging, it is also possible that leopard seals may have a significant influence on demographic rates by predating on them when birds are arriving at the colony. The dominant component of leopard seal diet at Bird Island is thought to be fur seals (Walker *et al.* 1998). As fur seals are and macaroni penguins were both highly abundant in the 1970s it does not seem likely that leopard seals changed their levels of predation from fur seals to macaroni penguins at this time. Finally, there are no records of killer whales predating on macaroni penguins at Bird Island. In other systems the exploitation of great whales has been linked to killer whales shifting their diets to smaller marine predators (Springer *et al.* 2003). If the removal of great whales from the Southern Ocean drove a switch in the dietary preference of killer whales in this region, the close correlation between the population trajectories of fur seals and macaroni penguins at Bird Island, in addition to the higher energetic return of predating on fur seals, would make them a more likely prey choice than macaroni penguins.

Limitations

Despite the many generalisations of the CJS model, the effect of birds permanently emigrating from a population remains unexplained within the framework. If a marked bird fails to be recaptured (within the study period), it will still be assumed dead within the model, irrespective of emigration or PIT tag loss. It is possible to overcome the issue of emigration using observations at multiple sites or dead recovery data (Sidhu *et al.* 2007; Ratcliffe *et al.* 2008), however the magnitude of the problem is really dependent on how site-faithful birds are and how this varies with competition, predation, life-stage and environmental conditions (Ims and Hjermann 2001; Weisser 2001; Dugger *et al.* 2010). Inter-species variation in breeding site fidelity has been noted in penguins (Williams and Rodwell 1992), although it is generally assumed that once they start to breed they remain relatively site faithful (Williams 1995). Natal fidelity, on the other hand, between fledging and recruitment, tends to be lower (Williams 1995). This may result in an underestimation of juvenile survival rates, but should not have affected our conclusions on the relative importance of the different drivers because it is unlikely that natal dispersal varied between years. Temporary migration associated with missed breeding is uncommon in macaroni penguins, but can occur in response to adverse winter conditions (Williams and Rodwell 1992). Although this will have little effect on the estimation of survival within a mark-recapture framework (Burnham 1993), it may cause the survival rates estimated by the population model developed in Chapter 5 to be biased low in particular years. It may be possible to overcome this issue by combining the mark-recapture and state-space population model in one framework, or by incorporating a rate of missed breeding into the productivity function. Because missed breeding in macaroni penguins does not occur at a constant rate, this latter approach would require the drivers of year-to-year variation to be identified.

A previous study using PIT tags and flipper bands to mark little penguins (*Eudyptula minor*), estimated the probability of PIT tag loss to be approximately 5% during the first year after marking (Dann *et al.* 2014). The use of flipper bands to mark penguins was discontinued by the British Antarctic Survey following anecdotal evidence of links between banding and reduced survival rates. Consequently, rates of PIT tag loss for this study are not known. In contrast to the Dann *et al.* (2014) study, the PIT tagging protocol at Bird Island involves the application of wound glue to seal the wound made by the transponder injection. The application of the tag loss values published by Dann *et al.* (2014) to the estimates of survival made here may therefore be inappropriate. It may be

possible to estimate a colony-specific rate of tag loss for Bird Island by externally marking birds with dye at PIT tagging, and manually recapturing individuals; the exact rate is likely to be less than 5% (Dann *et al.* 2014).

A well-recognized problem with the concepts of top-down and bottom-up control is that they are difficult to separate in practice, and in many situations some form of combined resource (bottom-up) and predatory (top-down) control is operative (Pace *et al.* 1999). Although the integrated population model developed in Chapter 5 was highly revealing, it was not possible to truly separate the predation pressure variable from also representing indirect and direct linkages with environmental variability. Model selection of candidate covariates was also limited by not being able to implement formal model selection within the state-space structure. To select candidate covariates in the survival and productivity process models during the integrated analysis would require methodological advances and further long-term data collection.

Future directions

During the course of this project a number of interesting questions have arisen that I have been unable to address, either because of a lack of time, data or appropriate analytical techniques. This thesis ends therefore with a brief overview of the ways in which themes covered during this project may be developed further.

1. Separation of the direct effects of predation from environmental drivers.

This may be undertaken by investigating how giant petrels utilise different on-land prey resources during the breeding season (i.e. fur seal carcasses, penguins; Bonner and Hunter 1982; González-Solís *et al.* 2000). Whilst giant petrels show species and gender driven segregation of foraging areas (González-Solís *et al.* 2000), it is unknown how this translates on-shore during times of elevated resource, such as the synchronised fledging of penguin chicks. Investigation of the drivers of population productivity in the two species of giant petrel and how these induce year-to-year variation in penguin survival rates could also elucidate interactions between bottom-up and top-down control.

2. To identify the mechanism that increased survival rates of macaroni penguins between 1985 and 2012.

This study could not attribute the increase in survival to an individual covariate (Chapter 5). The identification of the mechanism that has driven the survival rates of macaroni

penguins to increase would enable the linear term in the function models of survival to be replaced (Chapter 5), and enable scenario testing within this framework.

3. Krill fishery vs. predator-induced top-down control of krill biomass

To calculate the estimated contributions of predators vs. fisheries to krill biomass at South Georgia is dependent on verifying the overall trend of krill density for this region (Atkinson *et al.* 2004; Hewitt *et al.* 2003; Fielding *et al.* 2014). This would also require having a better understanding of the processes that determine krill recruitment, aggregation and retention at South Georgia (Loeb *et al.* 1997; Constable *et al.* 2003; Hewitt *et al.* 2003; Atkinson *et al.* 2004).

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Appendix

S1. Number of macaroni penguins PIT tagged and recaptured by season. Annual population size and productivity also shown.

Season	Total no. birds tagged >1 yr. old	Total no. fledglings tagged	Total no. individuals recaptured by gateway	Total d gateway in operation	Total no. individuals recaptured manually	Colony size	
						No. breeding pairs	No. chicks fledged
2003	114	76	-	-	-	536	315
2004	362	106	113	148	0	463	264
2005	151	118	431	154	0	537	272
2006	16	102	535	158	0	365	181
2007	52	100	0	0	79	527	243
2008	0	100	554	146	158	521	367
2009	90	120	470	14	175	511	372
2010	27	100	604	110	0	431	212
2011	90	96	599	120	1	409	263
2012	64	152	630	150	422	493	237
Total	966	1070	3936	1000	835	-	-

S2. Temporal resolution of environmental covariates.

No.	Covariate	Study period	Time lag (years)	Parameter
1	Local sea surface temperature anomalies (LSST)	Annual (October *t-1* to September *t*)	0	$LSST_0$
		Annual (October *t-2* to September *t-1*)	1	$LSST_{-1}$
2	El Niño/Southern Oscillation Index (ENSO)	Summer (October *t-3* to March *t-2*)	2	$ENSO_{-2}$
		Summer (October *t-4* to March *t-3*)	3	$ENSO_{-3}$
3	Southern Annular Mode index (SAM)	Summer (October *t-1* to March *t*)	0	SAM_0
		Summer (October *t-2* to March *t-1*)	1	SAM_{-1}

S3. Model selection for the global model structure. Examination of age class and maximum age of transition.

Model	AIC_c	ΔAIC_c	k	Model deviance
$\phi_{a3\,a*t/a*t}\ p_{0/t}\ \Psi_{3/0}$	1843.69	27.32	40	1785.35
$\phi_{a3\,a*t/a*t}\ p_{0/t}\ \Psi_{4/0}$	1847.66	31.29	41	1820.37
$\phi_{a1\ t}\ p_{0/t}\ \Psi_{4/0}$	1849.85	33.48	24	1911.70
$\phi_{a1\ t}\ p_{0/t}\ \Psi_{3/0}$	2018.63	202.26	23	1982.50

Notes; Model fit is assessed using the lowest AIC_C, with the difference between the best candidate model (Table 2) and other models specified (ΔAIC_c). See Table 2 for notation details.

S4. Model selection, ANODEV and LRT tests. Testing for individual trait, top-down and bottom-up influence. Recapture and transition probabilities specified as Model 1 (Table 2).

Step	Model	k	ANODEV tests for cohort-level covariates			
			df	*F*	*P*	R^2
3	Mass + $ENSO_{-3}$ / $ENSO_{-3}$	12	1	0.70	0.41	0.04
3	Mass + μ Mass / .	12	1	0.90	0.35	0.06
3	Mass + $LSST_0$ / $LSST_0$	12	1	1.15	0.30	0.07
3	Mass + SAM_{-1} / SAM_{-1}	12	1	1.54	0.23	0.09
3	Mass + SAM_0 / SAM_0	12	1	2.24	0.15	0.13
3	Mass + $ENSO_{-2}$ / $ENSO_{-2}$	12	1	3.49	0.08	0.19
3	Mass + $LSST_{-1}$ / $LSST_{-1}$	12	1	5.89	0.03	0.28
4	Mass + $ENSO_{-3}$ / $ENSO_{-3}$ **	13	1	0.10	0.75	0.01
4	Mass + $LSST_{-1}$ / $LSST_{-1}$ **	13	1	0.72	0.41	0.05
4	Mass + SAM_{-1} / SAM_{-1} **	13	1	1.55	0.23	0.10
4	Mass + SAM_0 / SAM_0 **	13	1	1.79	0.20	0.11
4	Mass + $LSST_0$ / $LSST_0$ **	13	1	2.01	0.18	0.13
4	Mass + $ENSO_{-2}$ / $ENSO_{-2}$ **	13	1	4.12	0.06	0.23
5	Mass + Pred. + $LSST_0$ / Pred. + $LSST_0$	14	1	0.31	0.74	0.00
5	Mass + Pred. + $ENSO_{-2}$ / Pred. + $ENSO_{-2}$	14	1	1.65	0.23	0.03
5	Mass + Pred. + SAM_{-1} / Pred. + SAM_{-1}	14	1	2.88	0.11	0.18
5	Mass + Pred. + $ENSO_{-3}$ / Pred. + $ENSO_{-3}$	14	1	3.19	0.10	0.20
5	Mass + Pred. + SAM_0 / Pred. + SAM_0	14	1	7.40	0.02	0.36
6	Mass + Pred. + SAM_0 / Pred. + SAM_0 **	15	1	0.26	0.61	0.02
6	Mass + Pred. + SAM_{-1} / Pred. + SAM_{-1} **	15	1	0.47	0.50	0.04
6	Mass + Pred. + $LSST_0$ / Pred. + $LSST_0$ **	15	1	0.61	0.45	0.05
6	Mass + Pred. + $LSST_{-1}$ / Pred. + $LSST_{-1}$ **	15	1	0.73	0.41	0.06
6	Mass + Pred. + $ENSO_{-3}$ / Pred. + $ENSO_{-3}$ **	15	1	1.37	0.27	0.10
6	Mass + Pred. + $ENSO_{-2}$ / Pred. + $ENSO_{-2}$ **	15	1	2.77	0.12	0.19
6	Mass + Pred. + $LSST_{-1}$ + $ENSO_{-3}$ / Pred. + $LSST_{-1}$ + $ENSO_{-3}$	15	1	0.37	0.55	0.03

6	Mass + Pred. + $LSST_{-1}$ + SAM_{-1} / Pred. + $LSST_{-1}$ + SAM_{-1}	15	1	0.40	0.54	0.03
6	Mass + Pred. + $LSST_{-1}$ + $ENSO_{-2}$ / Pred. + $LSST_{-1}$ + $ENSO_{-2}$	15	1	0.60	0.46	0.05
6	Mass + Pred. + $LSST_{-1}$ + μ Mass / Pred. + $LSST_{-1}$ + μ Mass	15	1	0.61	0.45	0.05

Notes; Predation pressure (Pred.) included as an interactive effect with age class, and environmental covariates considered as additive with age class unless specified. ** step-up from an additive effect to an interactive effect with age class for the covariate being considered. Bottom-up covariates considered at specified lags. (μ Mass) annual mean of fledging mass.

S5. The estimated logit link function parameters for model 5: Table 3; Chapter 3.

Parameter	Parameter estimate	Standard error
Adult survival	2.13	0.08
Juvenile survival	-2.42	0.27
Fledging mass	0.54	0.19
Predation on adults	-0.16	0.10
Predation on juveniles	-0.87	0.33
$LSST_{-1}$	0.06	0.05

S6. Detailed methods

Preliminary model selection

Covariates selected for modelling survival followed the analysis of deviance results reported in Chapter 3 (Horswill *et al.* 2014). Model selection for fecundity was first undertaken by modelling years with a complete set of candidate covariates (n=11; Table 6) in a logistic Generalised Linear Model (GLM) in program R (v 3.0.2; R Core Team 2014). The model included all main effects, and the best candidate model was selected using a step-wise approach that ranked candidate models based on the second-order Akaike Information Criterion (AIC_c). The GLM drew information solely from the fecundity data, not the integrated population dataset, so it was postulated to be a conservative approach, retaining only those covariates with the strongest relationship to chick production.

Observation model

Survival estimates were assumed to have a normal error distribution on the scale of the linear predictor with a variance equal to the inter-annual average of 95% confidence intervals estimated by Horswill *et al.* (2014; Chapter 3). These confidence intervals were transformed to the logit-scale to estimate the variance of the normal distribution (fledglings = 0.07; birds >1-yr = 0.02). For fecundity, the estimated number of female chicks and the number of breeding female birds were also assumed to have normal error distributions on the scale of the linear predictor. The mean was equal to the point estimate of breeding females or female chicks. The precision was derived from the available data of repeated ground counts of breeding females. This data was available for 5 years between 2007 and 2012; after the population stabilised. The same variance was therefore applied to all years assuming that the observation error was independent of population size. The variance of the observation model (s^2) was calculated as a ratio mean annual variance ($\bar{\sigma}^2$ =1727.3) over the mean number of counts ($\bar{n}$ = 4.7 repeated counts):

$$s^2 = \frac{\bar{\sigma}^2}{\bar{n}} = 0.0028 \qquad \text{(A)}$$

Prior distributions

Prior distributions for the covariate coefficients were specified as rescaled beta distributions that gave uniform likelihood between values 0 and 1 (adapted from Matthiopoulos *et al.* 2013):

$$Y \sim Beta(1.0006,1.0006)$$
$$X = X_{\min} + Y(X_{\max} - X_{\min}) \quad \text{(B)}$$

The beta distribution was favoured over a uniform distribution because it enables prior densities to be concentrated around specified mean values if required. Incomplete time series of specific covariates required the use of informative priors where appropriate. The coefficients for the covariates of survival were given prior distributions that were constrained to be either positive or negative in line with published information on these effects (Chapter 3; Horswill *et al.* 2014). For example, within a given year the survival rate of fledgling birds has a positive relationship with fledging mass. The priors included zero so that the effect could also be cancelled during model fitting. The priors for the coefficients of the covariates of fecundity could be argued from published information on other Spheniscidae, but vague priors were used in accordance with published knowledge on this population. These were structured according to eqn. 2 with mean zero. The intercept terms ($\sigma_{f,t}, \sigma_{a,t}, \beta_t$) and the trend parameter that links the survival rates of the age classes (σ_t) were also given vague priors. For the intercept terms these were bounded between 0 and 1 on the non-linear predictor scale to enable meaningful probabilities to be estimated. The range for the trend parameter was set to be able to generate changes in survival from 1 to 0 over a period of 16-years on the linear predictor scale (equivalent to the duration of rapid population decline in our study). The auto-covariate (C) was generated as a state-variable in the model so it could not be standardised within the model framework. Because this covariate was on a much larger scale than the standardised covariates, the variances of the priors relating to this covariate were scaled accordingly (see supp. info. S2).

Missing data

Missing data on fledging mass and post-migratory condition were estimated as normal variates with an expectation equal the observed data. A normal distribution was used so that the predicted values could take positive or negative values in line with the standardised time series of covariate data. Predation pressure was modelled as a random walk through time to account for serial autocorrelation in the process:

$$P_{t+1} \sim Normal(P_t, \tau)$$
$$\tau \sim Uniform(1.51, 10\text{x}10^5) \quad \text{(C)}$$

Here, data points are estimated as normal variates with an expectation equal to the previous year (observed or estimated, P_t). The precision ($t = s^{-2}$) between sequential data points was given a uniform prior distribution from zero to the maximum observed precision between sequential data points (eqn. C). To verify that this precision could be considered as representative of the entire study period, the sequential difference was extrapolated according to full island censuses ($\bar{x} = 329.2, \sigma = 261.1$; BAS unpublished data) and compared to productivity data collected for the whole island between 1978 and 1982 ($\bar{x} = 331.8, \sigma = 240.1$; Hunter 1984). The first value of predation (P_{1985}) was assigned a rescaled beta prior with a mean and range equal to the observed data (see "Prior distributions"). The tails of the normal distribution in the random-walk model permit estimated values of predation pressure to become negative. Therefore the likelihood of this state was truncated at the standardised value of zero predation pressure. To estimate the minimum number of penguins predated, survival rates were imputed according to equations 2 and 3 in the main text and equations D and E detailed below. These functional equations were fitted simultaneously so that parameter estimation was identical:

$$\text{logit}(\phi_{f,t}) = \sigma_{f,t} + \sigma_1 t + \sigma_2 M_t + \sigma_5 S_{t-1} \quad \text{(D)}$$

$$\text{logit}(\phi_{a,t}) = \sigma_{a,t} + \sigma_t t + \sigma_5 S_{t-1} \quad \text{(E)}$$

Initialising the population size

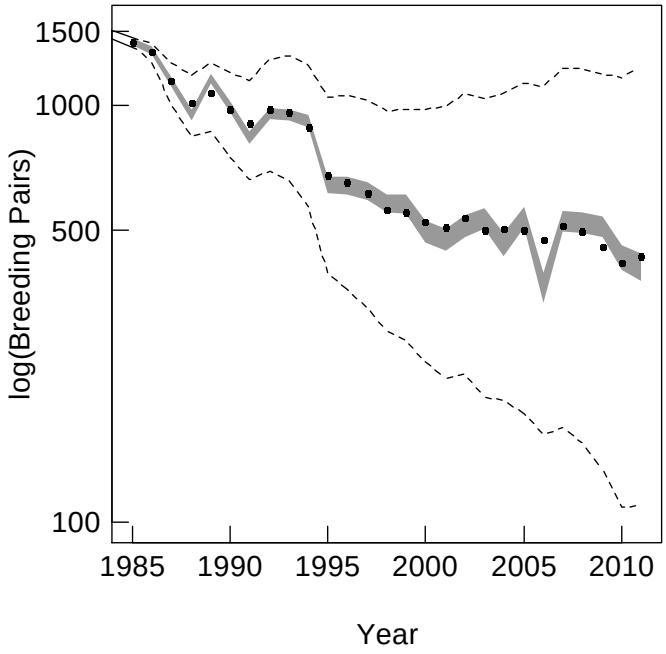
The possible error associated with the 1985 measurement of population size was estimated by comparing the mean ground count of breeding pairs with a photo of the entire colony taken at the same time. Corresponding photos were available for 5 years. Photo counts were repeated by 5 persons, and the average measurement error was estimated by subtracting the mean photo count from the mean ground count for each available year (±30 birds). This estimate of error was used initialise the population size from a uniform prior using the mean ground count for 1985.

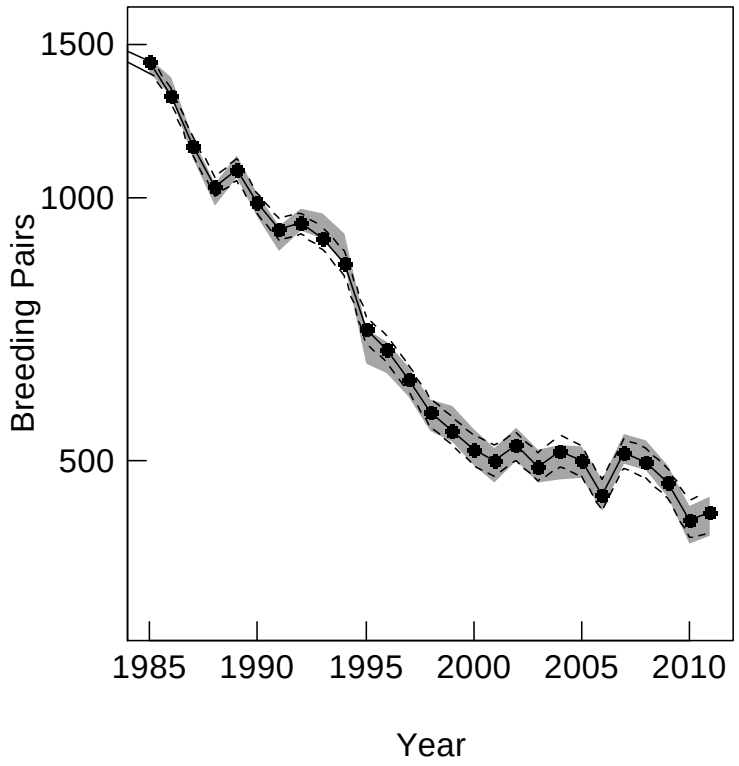
S7. Prior and posterior information on the integrated population model's parameters given on the logit-scale.

Parameter				Prior distribution		Posterior distribution	
Symbol	Demographic rate	Description	Type	Median	95-percentiles	Median	95-percentiles
$\sigma_{f,t}$	Survival	Baseline fledgling survival 1985	Beta	0.50	(0.00, 1.00)	-1.35	(-1.72, -0.97)
$\sigma_t t$	Survival	Regression coefficient for fledging and adult survival additive term	Beta	0.00	(-0.10, 0.10)	4.49×10^{-2}	(3.07×10^{-2}, 5.86×10^{-2})
$\sigma_{a,t}$	Survival	Baseline adult survival 1985	Beta	0.50	(0.00, 1.00)	1.23	(0.94, 1.54)
σ_2	Survival	Regression coefficient for effect of fledging mass	Beta	0.50	(0.00, 1.00)	0.21	(9.07×10^{-3}, 0.75)
σ_3	Survival	Regression coefficient for effect of predation pressure	Beta	-0.50	(0.00, -1.00)	-0.43	(-0.52, -0.35)
σ_4	Survival	Regression coefficient for interactive term between age class and predation pressure	Beta	-0.50	(0.00, -1.00)	-0.47	(-0.69, -0.24)
σ_5	Survival	Regression coefficient for effect of $LSST_{-1}$	Beta	0.50	(0.00, 1.00)	0.05	(2.09×10^{-3}, 0.16)
β_t	Breeding success	Baseline productivity 1985	Beta	0.50	(0.00, 1.00)	-0.83	(-1.06, -0.60)
β_1	Breeding success	Regression coefficient for effect of arrival mass	Beta	0.00	(-0.10, 0.10)	0.28	(8.64×10^{-2}, 0.51)

β_2	Breeding success	Regression coefficient for effect of $ENSO_{-2}$	Beta	0.00	(-0.10, 0.10)	-0.26	(-0.48, -4.14×10^{-2})
β_3	Breeding success	Regression coefficient for effect of intra-specific competition	Beta	0.00	(-0.10, 0.10)	-2.29×10^{-4}	(-5.40×10^{-4}, 5.51×10^{-5})
β_4	Breeding success	Regression coefficient for effect of predation pressure	Beta	0.00	(-1.00×10^{-3}, 1.00×10^{-3})	8.78×10^{-2}	(1.07×10^{-2}, 0.18)
β_5	Breeding success	Regression coefficient for effect of $LSST_0$	Beta	0.00	(-0.10, 0.10)	-2.97×10^{-2}	(-0.39, 0.33)
β_6	Breeding success	Regression coefficient for effect of interaction between intra-specific competition and $ENSO_{-2}$	Beta	0.00	(-1.00×10^{-3}, 1.00×10^{-3})	-2.07×10^{-4}	(-6.42×10^{-6}, 4.30×10^{-4})
β_7	Breeding success	Regression coefficient for effect of interaction between intra-specific competition and $LSST_0$	Beta	0.00	(-1.00×10^{-3}, 1.00×10^{-3})	-1.38×10^{-4}	(-2.72×10^{-4}, 5.29×10^{-4})

S8. Result of model validation exercise where the population trajectory of macaroni penguins at Bird Island, South Georgia, was simulated as a function of the parameter estimates and the covariate data only. Posterior median values (circles) and credible interval (dashed lines) are shown against the observed population trajectory with confidence interval estimated from the repeated counts (shaded grey).





S9. Sensitivity of the simulated population size to changes in the prior distribution used to model the missing values of predation pressure. The full model with credible interval ($\tau \sim Uniform(1.51,10x10^5)$ - grey band) and the model with decreased variance ($\tau \sim Uniform(10,10x10^5)$ - points). Scaling on the y-axis is $\log_e$, values are back-transformed.

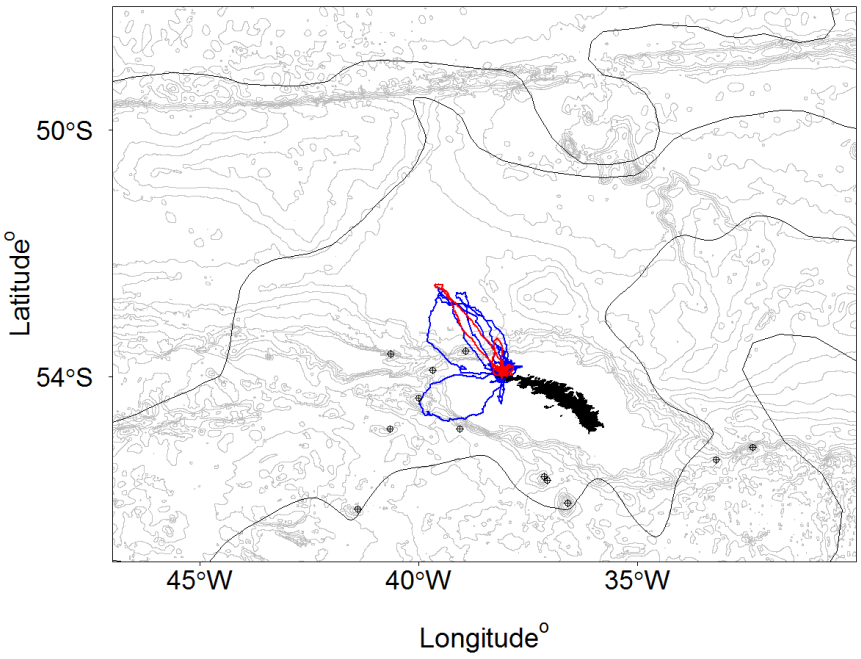
S10. Mean and standard deviation of demographic rates and covariates before and after the *c.* 2000 breakpoint in the population trajectory.

		Before 2000	After 2000
Survival (Fledging year)		0.41 ±0.19	0.42 ±0.20
Survival (>1 year)		0.86 ±0.06	0.89 ±0.04
Recruitment		0.10 ±0.05	0.12 ±0.04
Productivity	Female chicks female^{-1}	0.26 ±0.04	0.29 ±0.03
	Chicks pair^{-1}	0.51 ±0.08	0.57 ±0.06

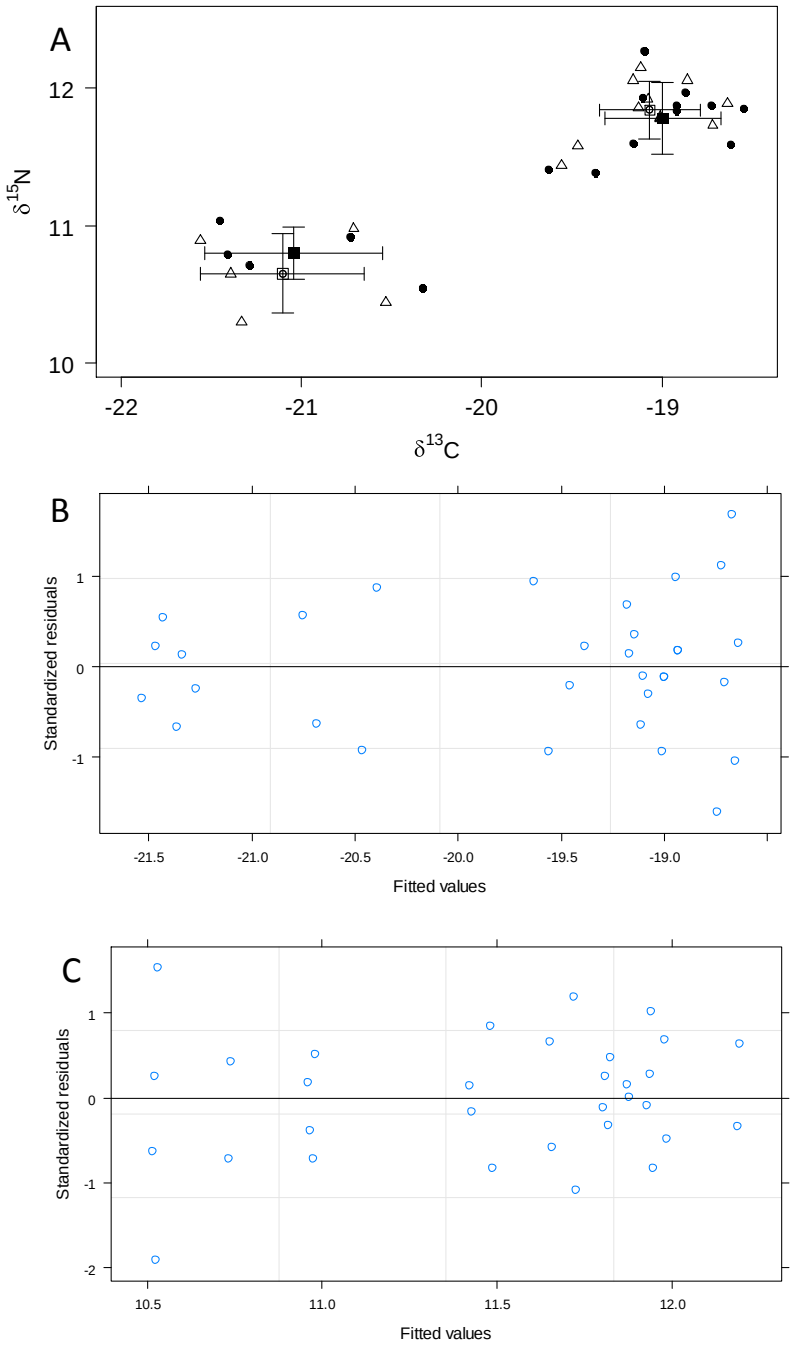
S11. Number of individuals within each dietary type by sex and time.

	Year	Period of synthesis	*n*		Individuals in each dietary type (*n*)							
			M	F	Type 1		Type 2		Type 3		Type 4	
					M	F	M	F	M	F	M	F
Feather	2001	Pre-moult	20	20	11	13	9	7				
	2002	Pre-moult	20	20	14	10	6	10				
	2003	Pre-moult	14	19	9	11	5	8				
	2011	Pre-moult	20	22	10	8	10	14				
	2012	Pre-moult	21	20	13	9	8	11				
Blood Plasma	2012	Winter	12	-	12	-	0	-				
		Incubation	7	15	7	9	0	6				
		Brood	-	9	-	0	-	9				
		Crèche	15	14	0	0	15	14				
		Pre-moult	16	14	8	6	8	8				
Guano	2012	Winter	8	2	8	2	0	0				
		Incubation	4	4	3	3	1	1				
		Brood	-	9	-	0	-	9				
		Crèche	4	8	0	0	4	8				
		Pre-moult	7	4	5	3	2	1				
Blood cells	2012	Winter	12	8	12	8	0	0	0	0	0	0
		Incubation	7	15	0	0	0	10	7	5	0	0
		Brood	-	9	-	0	-	8	-	1	-	0
		Crèche	15	12	0	0	15	3	0	0	0	9
		Pre-moult	14	13	0	0	5	4	0	0	9	9

N.B. Dietary types in blood cells are not comparable with other tissues.



S12. Comparison of the foraging distribution during the crèche period of 2002 (blue) and 2012 (red). Preliminary analysis to examine whether feather samples should be standardised. Max. distance travelled in 2002 = 187.39 km; Max. distance travelled in 2012 = 196.45 km.



S13. A) Difference between clean (black circles) and unclean (triangles) feathers; feathers collected in 2001/02. Standard deviations shown for clusters assigned by $\delta^{15}N > 11.25$. B) Standardised residuals for random effects model $\delta^{13}C \sim$cleaning. C) Standardised residuals for random effects model $\delta^{15}N \sim$cleaning.

Accompanying material